R 260 C1 [Ex. 2]

MÉMOIRES
DU MUSÉUM
NATIONAL
D'HISTOIRE
NATURELLE

ZOOLOGIE
TOME 140
1988

Alain DUBOIS

The genus in zoology: a contribution to the theory of evolutionary systematics

Source : MNHN, Paris

MÉMOIRES DU MUSÉUM NATIONAL D'HISTOIRE NATURELLE

Directeur de la publication : Philippe BOUCHET
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Rédaction : 57, rue Cuvier
75005 Paris

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Éditions du Muséum
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38, rue Geoffroy St-Hilaire
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Parution et prix irréguliers. Les ordres permanents d'achat et les commandes de volumes séparés sont reçus par le service de vente. Catalogue sur demande. Une liste des derniers titres parus figure en page 3 de couverture.

Volumes are published at irregular intervals, and at irregular prices. Standing orders and orders for single volumes should be directed to the Sales Offices. Free price list and catalogue on request. Recently published memoirs are listed on page 3 of the cover.

The Muséum national d'Histoire naturelle also publishes a Bulletin.

Source : MNHN, Paris

Bibliothèque Centrale Muséum
3 3001 00132122 2
Source : MNHN, Paris

Source : MNHN, Paris

The genus in zoology: a contribution to the theory of evolutionary systematics

English version.
This text also exists in French version :
Le genre en zoologie : essai de systématique théorique, *Mém. Mus. natn. Hist. nat.*, (A), **139** : 1-132 — Paris
ISBN 2-85653-152-0.

Source : MNHN, Paris

ISBN : 2-85653-151-2
ISSN : 0078-9747
© Éditions du Muséum national d'Histoire naturelle, Paris, 1988.

Source : MNHN, Paris

MÉMOIRES DU MUSÉUM NATIONAL D'HISTOIRE NATURELLE

SÉRIE A
ZOOLOGIE
TOME 140

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The genus in zoology: a contribution to the theory of evolutionary systematics

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DU MUSÉUM
PARIS
1988

Source : MNHN, Paris

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Abstract

DUBOIS, A., 1988.11.18. THE GENUS IN ZOOLOGY: A contribution to the theory of evolutionary systematics. Mém. Mus. natn. Hist. nat. (A), **140** : 1-124. Paris ISBN 2-85653-151-2.

(1) Despite its importance, both theoretical and practical, in animal systematics, the concept of the genus has until now been largely neglected by the theoreticians of classification. The present work offers a reflection on this concept and on related ones, and a detailed study of a new criterion proposed to define genera, that of hybridizability.

(2) The analysis proceeds within the framework of an " evolutionary " or " synthetic " conception of classification. It is suggested that genera should be defined as genetic, phylogenetic and ecological units, three concepts here made explicit. Thus defined, genera are discontinuous evolutionary units which exist really in nature, and not creations of the human mind.

(3) The problem of the genetic similarity between two organisms is studied in detail. The analysis presented insists upon the importance of the rôle of regulatory genes in the morphological evolution of organisms and in the phenomena of speciation, as well as on the independent evolution of regulatory genes from that of structural ones. It follows that criteria like " genetic distance ", which measure the divergence between organisms at the level of structural genes, are of little use for the construction of an evolutionary classification. Rather, classification must rely upon synthetic criteria, such as those derivable from the analysis of the morphology, or also from the study of interspecific hybridization.

(4) It is to be hoped that in the future evolutionists and systematists will grant more importance than thus far to the study of interspecific hybridization, of its mechanisms and consequences, in a double perspective: analysis of evolutionary phenomena in zoology, and applications at the level of supraspecific classification. Most attention should be devoted to the *positive* results of interspecific hybridization, which have a clear meaning (criterion of functional genetic similarity, and proof of a common phylogenetic origin of the hybridized species); in contrast negative results are of little interest to systematists. The concept of " hybrid distance " deserves review in the light of the present suggestions and of the works already achieved in this field by Gregory S. Whitt and his co-workers; the results obtained with this index should be compared with those generated by other comparative techniques. It is likely that such comparisons with other types of interspecies " distances " (phenetic, " genetic " or molecular, cladistic, karyological, eco-behavioural distances) will provide interesting lessons about the modalities of animal evolution.

(5) Review of the major results drawn from the study of both natural and experimental hybrids in the animal kingdom, and of the relations which exist between these results and the other available data concerning animal species, leads to the proposal of the new criterion of hybridizability to identify genera in zoology: whenever two species can give viable adult hybrids, they should be included in the same genus; if other valid criteria had led them previously to be placed into different genera, these must be merged.

(6) The criterion of hybridizability is a *relational taxinomic criterion*. Such criteria rely on the characteristics of the *relations* between the organisms that are compared. They differ from traditional *taxinomic characters*, which are gathered on the organisms taken separately and later compared " from the outside ", in the mind of the observer. It is suggested that such relational criteria may play an important rôle in " evolutionary " or " synthetic " systematics, although they have thus far been neglected in favor of the " analysis of characters ", and that they deserve a more thorough theoretical and practical investigation.

(7) The new criterion gives the genus category a deep biological and evolutionary meaning and makes possible a standardization of supraspecific systematics in the whole animal kingdom. Better than other possible criteria, it provides a partial solution to the problem of the equivalence of higher taxa among different groups.

(8) The consequences of the application of this criterion to the current classifications of the five major classes of gnathostome vertebrates are examined, in the light of Van Valen's (1973) metataxinomic criterion. This study suggests that application of this criterion would have much more important consequences in some groups (like birds) than in others. It would be beneficial, as permitting the suppression of some biases of the current classification, due in particular to the overestimation of the importance of certain characters. Other arguments in favor and in disfavor of the use of this criterion are studied.

(9) The mechanisms responsible for the birth of a new genus (geniation) are discussed. Genera appear discontinuous in nature, in morphological, genetic and ecological terms. It is proposed that most geniation phenomena involve speciations by genetic revolution,

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within small isolated founder populations. The notions of genetic revolution and of transilience are discussed. The importance of regulatory genes in the processes of geniation by genetic revolution is emphasized. These phenomena occur on the level of populations and do not involve the sudden emergence of individual "hopeful monsters". The study of the mechanisms of geniation may permit an objective estimate of the respective importance of genetic revolution and other mechanisms in these events.

(10) Finally, the taxinomic categories between the genus and the species (superspecies, ultraspecies, species complex, species group, synklepton, subgenus) are discussed, and examples of the use of these various categories are offered in the class of Amphibia.

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RÉSUMÉ

DUBOIS, A., 1988.11.18. THE GENUS IN ZOOLOGY: A contribution to the theory of evolutionary systematics. Mém. Mus. natn. Hist. nat. (A), **140** : 1-124. Paris ISBN 2-85653-151-2.

(1) Malgré son importance, théorique et pratique, en systématique animale, le concept du genre a été jusqu'à nos jours largement délaissé par les théoriciens de la classification. Le présent travail est consacré à une réflexion sur ce concept et les concepts voisins, et à l'étude détaillée d'un nouveau critère proposé pour définir les genres, le critère d'hybridabilité.

(2) Nous plaçant dans l'optique de la conception « évolutionniste » ou « synthétique » de la classification, nous préconisons de définir les genres comme des unités génétiques, phylogénétiques et écologiques. Ces trois concepts sont explicités. Ainsi définis, les genres constituent des unités évolutives discontinues qui existent réellement dans la nature, et non pas des créations de l'esprit humain.

(3) Le problème de la similitude génétique entre deux organismes est étudié en détail. L'analyse présentée insiste sur l'importance du rôle des gènes de régulation dans l'évolution morphologique des organismes et dans les phénomènes de spéciation, ainsi que sur l'indépendance de l'évolution des gènes de régulation par rapport à celle des gènes de structure. Il résulte de cette analyse que les critères tels que la « distance génétique », qui mesurent la divergence entre organismes au niveau des gènes de structure, sont de peu d'utilité pour la construction d'une classification évolutionniste. Celle-ci en revanche doit reposer sur des critères synthétiques, comme ceux que permet de dégager l'analyse de la morphologie, ou encore l'étude de l'hybridation interspécifique.

(4) Il est à espérer que dans l'avenir les évolutionnistes et systématiciens accorderont plus d'importance qu'ils ne l'ont fait jusqu'à présent à l'étude de l'hybridation interspécifique, de ses mécanismes, de ses conséquences, dans une perspective double : analyse des phénomènes évolutifs en zoologie, applications au niveau de la classification supraspécifique. A cet égard, il sera fondamental d'accorder la plus grande attention aux résultats *positifs* de l'hybridation interspécifique, qui ont une signification claire (critère de similitude génétique fonctionnelle, et preuve d'une origine phylogénétique commune des espèces hybridées), alors que les résultats négatifs sont de peu d'intérêt pour les systématiciens. Il sera indiqué d'explorer le concept de « distance hybride », à la lumière de nos suggestions et des travaux déjà effectués dans ce domaine par Gregory S. WHITT et ses collaborateurs, et de confronter les résultats obtenus au moyen de cet indice avec ceux fournis par d'autres techniques de comparaison des organismes. Il est probable que la confrontation de cette distance avec les divers autres types de « distances » susceptibles d'être mesurées entre espèces (distances phénétique, « génétique » ou moléculaire, cladistique, caryologique, éco-éthologique) sera riche en enseignements sur les modalités de l'évolution animale.

(5) Après un rappel des principaux résultats tirés de l'étude des hybrides, naturels et expérimentaux, dans le régne animal, et des relations qui existent entre ces résultats et les autres données dont on dispose sur les espèces animales, un nouveau critère, le critère d'hybridabilité, est proposé pour reconnaître les genres en zoologie. Il est suggéré que lorsque deux espéces peuvent donner naissance entre elles á des hybrides adultes viables, ces deux espéces doivent être incluses dans le même genre ; si ces deux espéces étaient auparavant classées, sur la foi d'autres critéres valables, dans deux genres distincts, ceux-ci doivent être réunis.

(6) Le critère d'hybridabilité est un *critère taxinomique relationnel*. De tels critères s'appuient sur les caractéristiques des *relations* entre organismes comparés. Ils s'opposent en cela aux *caractères taxinomiques* traditionnels, qui sont recueillis sur les organismes pris séparément et comparés ensuite « de l'extérieur », dans l'esprit de l'observateur. Il est suggéré que de tels critères relationnels peuvent jouer un rôle important en systématique « évolutionniste » ou « synthétique », oú ils ont été jusqu'á présent négligés au profit de l' « analyse des caractéres », et qu'ils devraient faire l'objet d'un examen, théorique et pratique, plus approfondi.

(7) Le nouveau critére donne á la catégorie de genre une profonde signification biologique et évolutive et rend possible une homogénéisation de la systématique supraspécifique dans l'ensemble du régne animal, permettant ainsi, mieux que les autres critéres envisageables pour une telle opération, de résoudre partiellement le problème de l'équivalence des taxons supérieurs entre groupes différents.

(8) Les conséquences de l'application de ce critére aux classifications actuelles des cinq principales classes de Vertébrés Gnathostomes sont examinés, notamment á la lumiére du critére métataxinomique de VAN VALEN (1973). Il est conclu que cette application, dont les conséquences seraient bien plus importantes dans certains groupes (comme les Oiseaux) que d'autres,

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serait bénéfique, car elle permettrait de supprimer certains biais de la classification actuelle, dus notamment à la surestimation de l'importance de certains caractères. D'autres arguments en faveur et en défaveur de l'emploi de ce critère sont étudiés.

(9) Pour finir, les mécanismes responsables de la naissance d'un nouveau genre (génération) font l'objet d'une discussion. Il est constaté que les genres sont discontinus dans la nature, en termes morphologiques, génétiques et écologiques. Il est proposé que la majeure partie des phénomènes de génération se produisent à l'occasion de spéciations par révolution génétique, au sein de petites populations fondatrices isolées. Les notions de révolution génétique et de transilience sont discutées. Le rôle important des gènes de régulation dans les processus de spéciation par révolution génétique est souligné, ainsi que le fait qu'il s'agit d'événements populationnels, et non de l'émergence brusque de « monstres prometteurs » individuels. Il est à espérer que dans l'avenir des travaux seront consacrés aux mécanismes de la génération et permettront d'estimer de manière objective l'importance respective des phénomènes de révolution génétique et d'autres mécanismes éventuels dans ces événements.

(10) Finalement, les catégories taxinomiques entre le genre et l'espèce font l'objet d'une discussion, et des exemples d'emploi de ces diverses catégories sont donnés dans la classe des Amphibiens.

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INTRODUCTION

Brief historical survey

This work has its origin in a strange observation. Having demonstrated, during a study of the amphibians of the Himalayan region (Dubois, 1974 a, 1975, 1976), the existence of a well defined group of closely related species of Ranidae, characterized by a peculiar ecology, I felt it necessary to name this group, and I wondered about the taxinomic[1] rank which should be given to it: "Genus, subgenus or species group?" (Dubois, 1976: 27). When I looked at the existing scientific literature, I realized with surprise how few publications had been devoted to a study of the genus concept (and of related concepts) in zoology. At this date and after a long bibliographical search, I know of only 42 publications bearing the word "genus" (or "subgenus") in their title, and dealing with this concept: Cope, 1868; Clark, 1911; Alphéraky, 1912; Metcalf, 1915; Pia, 1920; Schenck, 1937; Bartlett, 1940; Camp, 1940; Greenman, 1940; Sherff, 1940; Hubbs, 1943; Mayr, 1943, 1965; Simpson, 1943; Williams, 1951; Edwards, 1953; James, 1953; Cain, 1954, 1956; Mandelbrot, 1956; Paclt, 1957; Inger, 1958; Tortonese, 1962; Voous, 1964; Beck & Beck, 1968; Illies, 1970; Rowell, 1970; Clayton, 1972; Moore, 1976; Duellman, 1977; Van Gelder, 1977; Alberti, 1978; Bock & Farrand, 1980; Dubois, 1981 a, 1981 c, 1982 a, 1988; Plateaux, 1981; Bernardi, 1983; Daget, 1983; Stoyan, Stoyan & Fiksel, 1983; Lemen & Freeman, 1984. In addition, a few interesting discussions concerning this problem appeared occasionally in some general books (e.g.: Mayr, Linsley & Usinger, 1953; Simpson, 1961; Mayr, 1969, 1982 a; Crowson, 1970; Ross, 1975) or in papers on taxinomy (revisions, faunas, etc.) or on general zoology, where they are difficult to trace (e.g.: Ghigi, 1936; Montalenti, 1938; Ripley, 1945; Simpson, 1945; Inger, 1954; Laurent, 1956, 1964, 1972, 1973; Michener, 1957; Sibley, 1957; Cain, 1958; Savage, 1958; Johnsgard, 1960; Parkes, 1961; Rosen & Bailey, 1963; Pasteur, 1964, 1982; Poynton, 1964, 1976; Kluge, 1966; Short, 1969; Lynch, 1970, 1971; Pépin *et al.*, 1970; Martin & Watson, 1971; Dubois, 1975, 1976, 1980 b, 1981 b, 1983 a, 1983 c, 1984 a, 1984 c, 1987 b; Gorham, 1977; McAllister & Coad, 1978; Avise & Aquadro, 1982; Sibley & Ahlquist, 1982).

The above list of references is certainly still incomplete (I would be grateful to anyone who could help me to complete it!), but the very fact that it could be built up and that it only counts a few dozen titles contrasts with the very high number of papers and books devoted to a discussion of the species concept (there certainly exist several hundred, or even more, scientific publications including the word "species" in their title); this seemingly anecdotal observation underlines the fact that the genus concept has attracted the attention of the theoreticians of zoological classification much less than did the species concept. However, the fact that, in the Linnaean system of nomenclature, the generic name is part of the Latin binomial attributed to all species, and therefore appears in every scientific paper dealing with living beings, gives this

1. I use the correct spelling "taxinomy" instead of "taxonomy", following Pasteur (1976) and Fischer & Rey (1983).

Source : MNHN, Paris

name an important rôle in systematics, certainly much more important than that of the names of higher taxa.

Having realized this deficiency, I then devoted several years to reflection on the genus concept in zoology and to a discussion of this question with various colleagues, either personally, or by letters, or during conferences, symposia, meetings, etc. I also read several lectures on this subject, and this gave me the opportunity for fruitful discussions. Several papers summarizing my ideas on this question have already been published (DUBOIS, 1981 a, 1981 c, 1982 a, 1983 a, 1988). At the same time, I have started applying the principles and criteria proposed on the basis of general theoretical arguments, in works dealing with the systematics of the Amphibia, my major field of research (DUBOIS, 1975, 1976, 1977 c, 1979 a, 1980 b, 1981 b, 1983 c, 1984 a, 1984 b, 1984 c, 1984 e, 1987 b). To the best of my knowledge, until now only one author has discussed my proposals in a publication, and briefly studied the consequences of the latter on the classification of a given animal group: this author is DAGET (1983), and the group concerned is that of bony fishes.

In August 1981, I discovered the papers of VAN GELDER (1977, 1978) where this author proposed to use a criterion of hybridization to identify genera in zoology. A similar suggestion had been made by myself (DUBOIS, 1981 a, 1981 c, 1982 a) and by PLATEAUX (1981) on 14 March 1978 at a round table of the French zoological Society in Paris (see DUBOIS, 1981 a). The convergence between the three proposals is most interesting: on the practical level, they all lead to the same result (combination in a same genus of all species liable to give birth to viable hybrids), although the theoretical reasons given by the three authors are appreciably different.

In this paper, I present my ideas on this question at the end of 1985, and I try to combine in a single reflection all the data, hypotheses and discussions which I was led to meet during this long search. This is certainly not a final word on this question, on which I hope a rich discussion will now develop.

PRESENTATION OF THE PROBLEM

Zoological classification in the Linnaean system is based on a number of categories, from subspecies to super-kingdom. A critical survey of this system, of the concepts and methods, has already been in progress for a long time. However the different categories have not all been subjected to an equivalent study. The most abundant literature has certainly been produced on the " species problem " (see e.g.: MAYR, 1963, 1970, 1982 a; BOCQUET, GÉNERMONT & LAMOTTE, 1976, 1977, 1980). The question of the " higher categories " (family and above) is currently the matter of a much debated discussion among systematists (references to this question may be found e.g. in DUPUIS, 1979 and MAYR, 1981, 1982 a). However the genus, a category which occupies an intermediate position between the species and the higher categories, has been largely neglected so far in these discussions.

As a matter of fact, for many zoologists the only taxinomic category which corresponds to a reality in nature is the species, and all the other categories are artificial. If this was true, there would be no point in attempting a theoretical approach of the genus concept. However, if one follows MAYR (1969, 1981, 1982 a) and others in recognizing that zoological classification does not have for its only function to be a method of identification, but should also provide a system of storage for information, a genuine biological theory which may be used as a basis for all kinds of comparative works, it would seem justified to devote some attention to this category, which plays an important rôle in supraspecific systematics.

The practical agreement which exists between specialists as to the delimitation of genera varies from one zoological group to another. In many groups, this agreement is poor, and this results in a great instability of the generic classification

Source : MNHN, Paris

and nomenclature. It is true that a similar phenomenon also exists for the higher categories. However, a fundamental difference exists between these and the genus: in the Linnaean system of nomenclature, the generic name is part of the Latin binomial given to every species, which makes the need for its stability particularly imperative.

In LINNAEUS' mind, an important function of the generic name was to relieve the memory (CAIN, 1958), by collectively designating a group of " related " or " similar " species. Nowadays, all systematists would probably agree on a definition of the genus as loose as this: " a genus groups together species closer to each other than to species of other genera ". There remains to define what is meant by " close ", and, according to the definition which will be given of this term, radically different conceptions of the genus will ensue. In other words, the whole " genus problem " boils down to deciding *which information* must be carried by the generic name.

Many systematists have dreamed of a classification of the animal kingdom in which the different taxa of a same category would be *equivalent* in the various groups of animals (i.e. a genus of butterflies would be equivalent to a genus of birds or of molluscs, etc.). The search for this equivalence has led some systematists to adopt simple, or even simplistic, criteria to define genera, which will be discussed below. This problem of the equivalence of taxa is a difficult one, because of the absence of common characters between different groups (see SCHAEFER, 1976), but it may not be insolvable, as we shall see.

Another problem related to the preceding one is that of the *reality* of higher taxa (BALL, 1983). The question may be put in the following way: are the taxa which zoologists recognize artificial groupings of individuals, i.e. entities made up entirely by biologists — or entities which really exist in nature, independent from the consciousness systematists may have of them? According to the answer which will be given to this question, different methodological imperatives will result for systematists. If biological taxa are creations of the human mind, it will be important to fix rules to establish them. Several types of criteria may then be chosen to reach this aim, but the choice of the best criteria will finally be determined by pragmatical considerations: if taxa have no proper existence in nature, the best classification will be the one which will make easiest the work of systematists, and possibly of other biologists (the most " practical " one, in the various meanings of this term). On the other hand, if taxa do exist in nature, independently from the idea we may have of them, the task of systematists will then be to find them, to recognize them, even if this is not easy, and if this does not necessarily facilitate the work of biologists later on (e.g. insofar as particular or heavy techniques must be called upon to recognize them).

MAYR (1982 a: 207-208) rightly emphasized the fact that this problem is partly semantic, and comes partially from the confusion which has long existed between the concepts of *category* and of *taxon*. A *taxon* is a group of organisms of any rank which is distinct enough to be worth naming and assigning to a given category. In terms of logics, a taxon is an *individual*, and the animal or vegetal organisms which constitute it are the parts of this taxon. On the other hand, a *category*, in the contemporaneous sense of this term, indicates a rank or level in a hierarchical classification. It is a *class*, the members of which are all the taxa which are ascribed a given rank.

Relying on this distinction, MAYR (1982 a: 208) writes:

> " The question, Are the higher categories real ? must thus be dissolved into two separate questions: (1) Are (most of) the groups (taxa) which we rank in the higher categories well delimited ? and (2) Is it possible to give an objective (nonarbitrary) definition of such higher categories as genus, family, or order ? The answer to the first question is clearly yes, but to the second one it is clearly no ".

According to this conception, which has often been defended and illustrated in the scientific literature, the classificatory process would consist in two steps: first the recognition of taxa (whatever the method used to do it), then the establishment of the rank of each taxon. Only the first of these two steps would really be " nonarbitrary ". The allocation of given ranks

Source : MNHN, Paris

to taxa would be made in particular on the basis of the *size of the divergence* between them. Such a conception implies that all taxa are fundamentally of the same nature, but fit into each other like in a nest of dolls: thus eventually a subgenus would be a " small genus " or a " nascent genus ", a genus would be a " nascent family ", etc.

At the level of the species, the key-category of the Linnaean hierarchy, application of this conception would be wrong: the subspecies, as it is now understood, is not a " small species "; it is not even, or not necessarily, a " nascent species ". Most contemporaneous systematists agree to say that the species category is not an invention of the human mind, but that it corresponds to an objective reality in nature. In other words, independently from the conception biologists may have of them, entities exist in nature which correspond to the species concept as biologists now define it, i.e. a " closed, or protected, gene pool " (BOCQUET, GÉNERMONT & LAMOTTE, 1976, 1977, 1980): to use again MAYR's (1982 a) words cited above, this definition is therefore " objective " and " nonarbitrary ". The task of systematists is then to *recognize* the species in nature and not any more to " create " species. In the scale of Linnaean hierarchy, the species would thus be a fixed point, the position of which would be given in an objective way; on the other hand, the position of the higher categories would be arbitrary, and there would be no point in trying to fix it in an objective manner.

Yet, the species is not the only systematic category liable to be defined in a rigorous and objective way. BERNARDI (1980) recently provided a study of several categories designated by this author as " the taxinomic categories of evolutionary systematics ". All these do not show the same interest or importance, but some of them, like the superspecies (" monophyletic group of entirely vicariant species ", BERNARDI, 1980: 385) and the prospecies (the vicariant species which together make up a superspecies), indisputably correspond to real entities in nature. In the case of categories like the species or the prospecies, the distinction made above between recognition (or delimitation) of the taxon and establishment of its rank is not warranted any more. The criteria which allow the recognition of the taxinomic unit and its attribution to a given category are the same ones.

Is such a criterion proper to the species category and to the categories just above and below the species, studied by BERNARDI (1980), or is it possible to recognize also natural units at a higher level in the Linnaean hierarchy? This would only be the case if it was possible to find objective, nonarbitrary criteria to define these taxa. Such criteria would allow, as in the case of the species or of the prospecies, to recognize concomitantly both the existence of the natural taxon and its taxinomic rank. The thesis which will be defended here is that such criteria exist and may be found: as concerns the genus category, on which the following discussion is centered, I propose the use of a new criterion, the success of interspecific hybridization.

Before discussing this point, however, it is useful to make a rapid survey of the four major types of concepts of the genus category which may be found in the literature, so as to be able to place the new proposal within this general frame.

Source : MNHN, Paris

THE CONCEPTS OF THE GENUS

EMPIRICAL CONCEPT

An empirical concept of the genus underlies the practice of many systematists, who consider that there is no need for a theory of the genus. For these authors, the genus is only a practical convention, genera are pigeonholes which make the identification of species easier. Therefore the genus does not correspond to a real unit in nature, it is a creation of the mind.

These authors insist upon the fact that the genus must be useful, " pratical ". This notion of " practical ", however, is not clear. Does it mean " easy to recognize "? or " easy to identify "? " not too large "? " bringing such or such type of information "?

For many systematists, the criterion of *size* is given pre-eminence, which may be expressed by saying that " a genus must contain neither too many nor too few species ". These authors tend then to group together the isolated species in artificial genera, and to break up large genera, in order to obtain finally a mean number of " pigeonholes " of similar " volumes ".

A few authors are in favor of genera of a rather large size:

> " I personally feel that one should use rather large genera, such a solution being preferable in general biology, where scientific names of animals must be familiar to the largest number. " (BERNARDI, 1983: 136; translation mine).

Other systematists, probably more numerous, recommend on the contrary to reduce the size of genera as much as possible:

> " When a genus contains a large number of species and that it is possible to recognize within it natural groups by whatever means, it is desirable to split it in several genera. " (LAURENT, 1956: 230; translation mine).
>
> " In entomology there is sentiment in some quarters for setting an upper limit (perhaps 40) to the number of species allowed in a single genus. " (ROSS, 1975, cited by VAN GELDER, 1977: 2).

ROSEN & BAILEY (1963) have stressed the fact that, as the systematics of a group develops, one may often observe the following phenomena: first discovery, description and counting of the species; then tendency to " put order " in this mass of species and to group these together by affinities. The authors then often tend to create a genus for any group of species that may be shown to be closely related, and to break up genera as soon as new heterogeneities are disclosed in them. Eventually, they tend to recognize smaller and smaller, often monospecific, genera.

Such a practice denotes a misunderstanding of the fundamental meaning of the Linnaean binomial, where both names have different functions, the specific name expressing the singularity, and the generic name the existence of a group of

Source : MNHN, Paris

units which are "close" (or "similar", or "related", or both). The genus, contrary to the species, is a collective unit, and the first function of the generic name is to express similarity, not difference. The generic name as it is conceived by the splitters does not carry information any more, or hardly so:

> "This difference in the functions of species and genus names is completely ignored by many recent taxonomists, particularly the so-called generic splitters. It is their aim to express difference not only in the specific, but also in the generic name. This tendency, if carried to its logical extreme, leads to uninomialism, and some of the leading generic splitters have openly or in a veiled form endorsed this principle of nomenclature. To me it seems to indicate a complete misunderstanding of the principle of binomial nomenclature, if somebody uses the generic name primarily to express difference. This is the function of the species name." (MAYR, 1943: 138).

It is useful in this respect to reproduce the following extract of the work of ROSEN & BAILEY (1963) on poeciliids, where similar ideas are expressed very clearly:

> "It is evident that the phylogenetic relationships between different species or between distinct groups of species are reflected in a host of features, some anatomical and behavioral, some physiological and biochemical, and some genetic and developmental — in short, in some features of all the major systems and processes that characterize organisms. Hence, investigators in the fields of comparative anatomy and comparative development, as well as many experimental biologists, may contribute directly and indirectly to systematic knowledge. For the non-systematist, however, a classification consisting of too many small genera presents a major obstacle to his efforts at recognizing differences and similarities between related organisms that are worthy of study. In an earlier classification of the poeciliids, for example, two species now shown to be intimately related were placed in different genera because one of them possesses an asymmetrical external genitalium. Under this taxonomic arrangement, a developmental biologist interested in problems of asymmetry and hence in the asymmetric species would have difficulty identifying the symmetrical relative, the comparative study of which might be expected to yield important clues as to the origin of the asymmetric condition. The use of separate genera is usually, and justifiably, taken as a mark of the gross genetic incompatibility of the species thus separated taxonomically, and in the foregoing example may be expected to draw attention away from important biological properties common to both. It may even, at times, tend to prevent experimental workers from realizing that the comparative study of both species is appropriate. When a single genus is used for these species, the comparative materials are collected together, and the likelihood is increased that studies in other fields will be performed by investigators whose results are important to systematics. In general, the masking effects of an oversplit classification may be remedied by the use of comprehensive genera that assemble, and thereby underscore, some contrasting features as well as the many unifying characters to be found among intimately related organisms. The function of broad and coordinate genera, when data on complex and little-known groups are made available to non-systematists, is often overlooked by the taxonomist." (ROSEN & BAILEY, 1963: 6).

Source : MNHN, Paris

PHENETIC CONCEPT

If one admits that the genus must group together species which are "closer" to each other than they are to other such groups, what does the word "close" mean?

For the pheneticists, classification is based on the estimation or measurement of affinities, understood here in the sense of *phenotypic similarities*, which are in general supposed to represent genotypic similarities.

The old method, which can be traced to the early stages of systematics, consists in comparing the morphology of species, and in using these data for estimating, more or less subjectively, their resemblance. The latter is sometimes, but not always, supposed to express their genetic likeliness and their affinity. The modern aspects of this method rely on biometry (quantification of characters) and more recently (in the last 20 years) on numerical taxinomy, which takes into account a high number of characters (SNEATH & SOKAL, 1973). These characters may be taken from the morphology, but also from the ecology, the behaviour, the chromosomes, etc., i.e. the analysis bears on the totality of the *holomorph* (HENNIG, 1950). This leads to the estimation of a "distance" between species, and all the distances between several species may be presented graphically, e.g. on a phenogram. Pheneticists have sometimes ascribed a given systematic level to a given level of morphological "divergence": thus, two groups of species separated by such a distance will by definition be considered as two genera, by such another distance as two families, etc.

This leads to the grouping together of similar species. In general this resemblance is due to the common presence, in these species, of characters retained from a recent common ancestor. But this is not always the case. The resemblance may be due to the existence of a remote common ancestor, a *parallel evolution* having taken place, as a result of the presence at the start of genetic factors common to two long separated stocks. The resemblance may also be due to a *convergence* between different lineages, when these tend to adapt to similar modes of life.

The numerical methods of measurement of phenotypic similarities recently developed are valuable because they allow an objective, or almost so, estimate of the resemblance between two types of organisms, but they alone do not allow for the construction of a classification of living species. Such methods would be sufficient to classify objects, but not living beings which are the result of a *history* and which live in an *environment*.

CLADISTIC CONCEPT

As has been stressed by several authors, and singularly MAYR (1974), it is important clearly to distinguish between two fundamental aspects in the works of HENNIG and his disciples. The aim of *cladistic analysis* is to reconstitute as accurately as possible the phylogeny of a given group (establishment of a cladogram). Remarkable progress has been achieved in this domain by the cladists through the elaboration and formalization of principles and methods of work, some of which had been applied already long before HENNIG but in a much less systematic and rigorous manner. All zoologists who are interested in the study of phylogeny must become acquainted with the works of HENNIG and his disciples in this domain, and it is surprising that a few works are still published on these questions (CLARK, 1977; BLANDIN, 1978), where the con-

Source : MNHN, Paris

cepts and methods of the cladist school are not even mentioned. The works by DUPUIS (1979, 1984), which offer an almost complete list of the significant references in this field, may be consulted fruitfully in this respect.

The principles of *cladistic classification*, on the other hand, do not at all ensue directly from the preceding analysis. They constitute in reality a set of arbitrary rules and conventions aiming at the automatic transcription of the phylogeny into a classification.

As a matter of fact, for the cladists classification must only be a transcription, as exact as possible, of the phylogenetic tree or cladogram on another level. The rules adopted for this transcription are relatively simple. First, any new cladogenesis automatically gives birth to two new taxa. Then, only a taxon which contains *all* the descendants of a given ancestral species and this species itself is considered monophyletic. Finally the cladists have looked for a simple criterion making all taxa equivalent in different groups: it has thus been proposed that the rank of a taxon be automatically given by its age, or by the number of cladogeneses having taken place since its appearance. While classical methods of determination of the age of taxa posed important problems (see e.g. the discussion in DUPUIS, 1979: 47-50), SIBLEY & AHLQUIST (1982) recently suggested that DNA hybridization would allow the dating of cladogeneses in a relatively precise way. The use of such a criterion would lead for example to place all higher Primates in a single genus, or on the contrary to upgrade the frogs genus *Rana* to the rank of an order.

As far as they are concerned, systematists of the " synthetic " school (e.g. GISIN, 1964, 1966; MAYR, 1969, 1974, 1981), think that the cladist conception of classification, based on phylogeny alone, or rather on a restricted conception of phylogeny (considering only one of its aspects, cladogenesis), is singularly poor. As a matter of fact, cladist classification does not take into account the more or less important divergence between lineages which results from the existence of different rates of anagenesis between different lineages and at different epochs. Genealogical kinship and genetic similarity are not equivalent. A purely genealogical classification does not give any measure of the morphological, ecological and genetic resemblances between species. It does not take into account the transitions into novel adaptive zones, and the speeding up of evolutionary rates during these ecological shifts.

It may not be superfluous to point out that the criticism of some aspects of the " monophyletic " classification, i.e. based on genealogy alone, had been done in its broad lines very clearly and even before its birth by BIGELOW (1956: 146) in a forgotten passage which is worth quoting:

> " Without overlooking the fact that *resemblance reflects phylogeny*, it is well to bear in mind that *difference reflects evolution*, and that the nature and extent of these similarities and differences, not the time during which they have been retained or effected, is the primary concern of evolutionary classification. Organisms whose ancestors evolved very little relative to one another should not be separated merely because evolution has been slow, or grouped with organisms with whom they share a more recent common ancestry despite extensive overall differences that have evolved between them. Evolution is change, not time. If classification is to correspond with evolution, it must be based on the extent of overall difference, not on time. Monophyletic classification is based on *recency* of common ancestry (i.e. on time), and therefore should not be regarded as even a ' theoretical ' ideal. "

SYNTHETIC CONCEPT

For the generic name, which is part of the Latin binomial attributed to each species, to be useful, this name must contain the greatest amount of information possible, and an information distinct from that carried by the specific name. The three concepts of the genus that we have briefly reviewed above have in common the fact that the generic name carries in every case

Source : MNHN, Paris

little information or no information at all: no defined information for the empirists, information concerning the resemblance alone for the pheneticists, and the degree of kinship alone for the cladists.

The supporters of the " evolutionary " (MAYR, 1969, 1974, 1981), " synthetic " (GISIN, 1964; DUBOIS, 1981 c, 1982 a) or " quantic " (GISIN, 1966), school of classification, on the other hand, do not forget that the scientific name of species is meant to be used also by nonsystematists and must give them a synthesis of our knowledge on the evolution and the mutual relationships of groups. Although these three aspects are closely connected, it may be useful to consider separately three types of information which may be carried by the generic name: genera must be evolutionary units, i.e. genetic, phylogenetic and ecological units. We will now examine these three aspects in more detail.

THE GENUS AS A GENETIC UNIT

In his remarkable paper " Biological classification: toward a synthesis of opposing methodologies ", MAYR (1981) quite rightly explains that the classificatory process, according to the supporters of the " synthetic " school, is necessarily composed of several stages, and always begins by a phase of grouping " by inspection " the species considered " closer " to each other than they are to species belonging to other groups. For this work, empirical methods have long been used, but it is now possible to call upon the more elaborate methods of numerical phenetics alluded to above. As we have seen, these methods permit to group together " similar " species. In many cases, this resemblance stems from the existence of a strong genetic similarity between the species which are being compared. As far as the artificial groups due to evolutionary parallelism or to convergence are eliminated (see below), the units defined by such criteria may be interpreted as genetic units: at any rate it is only this hypothesis which justifies, in an evolutionary perspective, the grouping of species according to their morphological similarity.

Other criteria than morphological resemblance can be imagined for recognizing genetic units. One of these is the comparison of the proteins of the species studied, which leads to what is commonly called " genetic distances ". One of the unexpected results of the research in this field during the later years has been the discovery that morphological evolution and speciation on one hand, and protein evolution on the other, are largely independent, and that the study of the two categories of phenomena may sometimes lead to contradictory conclusions. The following question may then be posed: which of the two methods of estimation of the genetic similarity of two organisms is the most reliable, the most significant, one? Is it the measure given by what is commonly called " genetic distance ", which is based upon the characteristics of certain structural genes of the species studied, or the estimate given by the " phenetic distance " between these species, which is based on a more synthetic criterion, the global resemblance between the two phenotypes compared? We shall address this question in the next chapter, where we shall also examine another possible method of comparison of the genetic characteristics of two species, i.e. interspecific hybridization. At the moment we shall retain the traditional methods of study of genetic resemblance of animal species: in this respect it is clear that the oldest method, the overall comparison of the phenotypes of the species studied, remains by far the most generally used one by systematists. As we shall see below, this is not due only to the " laziness " or to the " lack of modernism " of systematists, but also to deeper causes: although it may seem strange to have to precise it, it is important to stress that, in many cases, the fact that two organisms have similar phenotypes is simply due to the fact that they have similar genotypes, because they share a common ancestor! We shall come back to this question.

Source : MNHN, Paris

The genus as a phylogenetic unit

The last sentences must not obscure the fact that the resemblance between two organisms may be due not to their having similar genotypes retained from a common ancestor, but to phenomena of convergence or of evolutionary parallelism. For all evolutionary systematists, it is clear and indisputable that a taxon can only be considered "natural" if it corresponds to a monophyletic group. This means that it is very important, in the construction of a classification, to try to eliminate as completely as possible artificial groups based on resemblances between species due to convergence and, less often, to evolutionary parallelism. This is the second of the stages described by Mayr (1981) in the building up of a classification. The methods to use in this respect were first described by Hennig (1950, 1966), then by his disciples, who have considerably refined them (see e.g.: Dupuis, 1979; Farris, 1979; Wiley, 1981). They are now part of the essential methods of all work of taxinomic revision, especially at higher levels.

With the help of these methods, the task of systematists is to try as much as possible to reconstruct the phylogeny, to break up all polyphyletic groups and keep only monophyletic groups.

A clarification is necessary here about the definition to give to the term "monophyletic". For a long time, no precise definition has been elaborated for this word, which was simply used to designate all groups composed of species descended from a same ancestor, i.e. all non-polyphyletic groups: this was consistent with the first proposal of this term by Haeckel (1868), who created "monophyletic" as opposed to "polyphyletic", and this was also consistent with the etymology of these words. Simpson (1961: 124) proposed the following definition:

> "*Monophyly is the derivation of a taxon through one or more lineages* (temporal successions of ancestral-descendant populations) *from one immediately ancestral taxon of the same or lower rank.*"

This definition is unacceptable for it is not rigorous enough and it is based on the ranks of taxa, i.e. on a criterion external to the phylogeny itself.

On the other hand, Hennig (1950, 1966) proposed a new definition of monophyly, which was reformulated by Wiley (1981: 76) as follows:

> "A *monophyletic group* is a group of species that includes an ancestral species (known or hypothesized) and all of its descendants."

This definition is rigorous and may be used to build up a classification according to cladistic principles. However by proposing it Hennig has stripped the word "monophyletic" of its initial sense (monophyletic being defined as opposed to polyphyletic), to give it a completely new sense (monophyletic being defined as opposed both to polyphyletic and to paraphyletic). This approach, which breaks with all anterior taxinomic tradition, has important consequences in classification, and it has been severely criticized by several synthetist authors (e.g. Mayr, 1974; Ashlock, 1980).

Because of the terminological confusion introduced by the cladists in this field, it has been necessary to coin new terms. Ashlock (1971, 1972, 1980), who devoted several excellent papers to the clarification of this question, proposed the new term of *holophyletic* to designate the concept called "monophyletic" by Hennig and his disciples. Even though, the cladists have continued to use the word monophyletic for this concept, while on the other hand synthetist authors use this word in its traditional sense. A considerable confusion ensues in the contemporaneous taxinomic literature, which has led Dubois (1986) to suggest abandoning completely the term monophyletic, to use holophyletic for "monophyletic *sensu* Hennig", and the new term *homophyletic* for "monophyletic *sensu*

Source : MNHN, Paris

ASHLOCK ". Four different terms, designating four different types of taxa, may thus be recognized. The following definitions are derived from those of ASHLOCK (1971, 1972, 1980), taking advantage of the remarks by FARRIS (1974), PLATNICK (1977) and WILEY (1979, 1981) (see fig. 1):

(1) A *homophyletic* group (monophyletic *sensu* ASHLOCK) is a group which contains the species which it its most recent common ancestor.

(a) A *holophyletic* group (monophyletic *sensu* HENNIG) is a homophyletic group which contains all the descendants of the species which is its most recent common ancestor.

(b) A *paraphyletic* group is a homophyletic group which contains only a part of the descendants of the species which is its most recent common ancestor.

(2) A *polyphyletic* (or heterophyletic) group is a group which does not contain the species which is its most recent common ancestor.

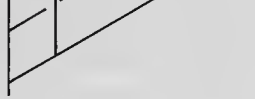

FIG. 1. — Phylogram illustrating the terms proposed by DUBOIS (1986). The vertical axis represents the time, the horizontal axis the divergence (in genetic, phenetic, ecological, etc., terms).
(1) Groups ABCDE, AC, BDE and DE are holophyletic (monophyletic *sensu* HENNIG).
(2) Groups AB, ABC and ABCD are paraphyletic.
(3) Group CDE is polyphyletic (heterophyletic).
(4) Groups of categories (1) and (2) are homophyletic (monophyletic *sensu* AHSLOCK).
(5) Groups of categories (2) and (3) are merophyletic.

Acceptation of the above terms and definitions, which would not necessarily imply agreement with one taxinomic school or another, would greatly help in the clarification of debates between the different schools, and therefore appear most justified. In such a perspective, cladists should admit that they try to recognize only holophyletic groups and that they reject as unnatural both polyphyletic and paraphyletic groups (merophyletic groups; DUBOIS, 1986). On the other hand, synthetists consider that all homophyletic groups *may* be natural, and that only the polyphyletic groups must always be rejected as unnatural.

As a matter of fact, how would the fact that a group has arisen from another group change the nature of the initial group? To use a famous example, if birds had never appeared, reptiles, including crocodiles, would be holophyletic. The appearance of birds makes them paraphyletic, but this does not in the least deprive reptiles from any reality: the latter remain a homophyletic group which corresponds to a defined " grade ". Quite irrelevant in this respect is the fact that birds, which correspond to a new grade and have conquerred a different adaptive zone, are issued from the same stock as crocodiles. As was well shown by MAYR (1974), the concept of paraphyletic groups is devoid, for the synthetists, of all interest in classification. This divergence is certainly, and by far, the most important one which exists between the cladist and synthetist conceptions of classification, which has not always been well perceived: many of the authors who have discussed cladism and compared it to the synthetic systematics have only touched lightly upon this problem and have even sometimes entirely omitted it. In the opinion of synthetists, the automatic rejection of paraphyletic groups stems from a methodological error, just like the generalization of formal notions like " sister groups ", " sister species ", etc., when in many cases it would be much more justified to speak of " child groups " or " child species ", etc.

For the synthetists, classification is based on the phylogenetic tree but is not a simple and automatic transcription of this tree: it takes additional information into account. Thus a same genus will be used to group species considered very close, according to their various char-

Source : MNHN, Paris

acteristics, and derived all from a common ancestor belonging to the genus. But this does not imply that all the descendants of this common ancestor be included in the taxon: as a matter of fact some of these descendants may have considerably diverged, and may not be " very close ", by their characteristics, to the cladistically related species; it will then be justified to create for them a different genus, or several.

The phylogenetic criterion allows therefore the separation, into distinct genera, of species which show important morphological resemblances, due for example to convergences, but which have different phylogenetic origins. On the other hand this criterion is insufficient in itself for deciding whether various species of the same phylogenetic origin must be grouped together in a same genus or not. For this purpose, it is also necessary to take into account other criteria mentioned above and below (genetic and ecological unit).

The genus as an ecological unit

Every species may be characterized by its *ecological niche*, a concept which refers to the various interactions between the species and its biotic and abiotic environment. Similarly, the higher taxa may also be characterized by their " niche ", which is " wider " than that of any of their included species.

Simpson (1944, 1953) proposed the phrase *adaptive zone* to designate the various relationships between groups of organisms and their environment. Huxley (1958) popularized the use of the term *grade* to designate the *levels of organization* corresponding to given adaptive zones. One may thus speak of the tetrapod grade, of the homeotherm grade, of the mammalian grade, etc. A grade is a group of organisms which possess in common a number of adaptive characteristics. A grade may be polyphyletic.

Inger (1958) proposed to define the genus as a group of closely related species occupying the same adaptive zone.

It is important to note that this criterion applies only after the preceding ones:

— within a homophyletic group (therefore within a single family);
— in agreement with the data concerning the genetic similarity of the species.

This criterion applies then within a group of species which are " obviously close " according to all other criteria, and among which (morphological) subgroups may be recognized, in order to try to establish whether these subgroups have or not attained a generic grade.

Such a conception of the genus implies necessarily that genera be separated by morphological gaps. It was already an old conception of the genus to admit that good genera must be separated by a *discontinuity*, i.e. that no *intermediate* species exist between them. It was often argued that the absence of these intermediate forms was due to their extinction. However Simpson (1961), while recognizing this fact, insisted that extinctions, by producing these gaps, were giving us a *nonarbitrary* criterion to define taxa. It may be added that, at least in many cases, extinctions *are not random*. The nonadaptive zone which separates two adaptive zones may only be crossed by transitory, short lived populations, which generally leave no fossils, and which exhibit a high rate of anagenesis, thus allowing genuine *evolutionary jumps*.

From a practical point of view, the problem is to find a way of recognizing that different groups of species occupy disjunct adaptive zones. The ideal would be to have precise data on the ecology of the species, and in this respect the works of ecologists may be most helpful to systematists. To tell the truth, until now ecologists have mainly devoted themselves to the concept of ecological niche (see Blondel & Bourlière, 1979) and to the comparison of ecologies of closely related species. One may however hope that, in the future, comparative works at higher levels, like those of Heyer (1973, 1974, 1976, 1979), Crump (1974), Barbault (1974 a, 1974 b, 1980, 1984), Inger & Colwell (1977), Duellman (1978) or Scott (1982), to take only examples in the fields of batrachology and herpetology, will develop. Such works could

Source : MNHN, Paris

allow a better knowledge of the characteristics of adaptive zones, and a more objective estimation of ecological resemblances and divergences between species of a same ecosystem or of various ecosystems.

Admittedly, this is yet still largely impossible, and, furthermore, for many groups of animals, field data are rare or even completely lacking. In such cases it will be necessary to infer from the sole morphology the adaptive function of characters. It goes without saying that such works may be carried out only by specialists of the group, having in particular a knowledge of the ecological characteristics of at least a part of its species. Clearly, in groups where ecological studies are difficult, as well as in paleontology (at least in the groups which are only known as fossils and for which comparisons with living species cannot be done), works of this type are difficult, if not impossible, to carry out.

In the absence of data, it may be useful to rely on the study of *convergences*: thus a character, or better, a set of characters, liable to appear independently in several lineages, in animals facing similar conditions of environment, is likely to be adaptive.

This criterion leads us to give more weight, in classification, to characters having a clear adaptive meaning than to those which do not have such a clear meaning. In the absence of any indication on its function, one should avoid recognizing a genus for animals which exhibit a somewhat special morphological character.

The works of INGER (1954, 1958), where the use of ecological criteria was suggested for better identification of genera, were not approved unanimously by specialists of amphibians, despite the most convincing examples given by this author. Some authors have accepted these proposals favorably and have sometimes applied them in their own works (POYNTON, 1964, 1976; LYNCH, 1970, 1971; MARTIN & WATSON, 1971; DUBOIS, 1975, 1976, 1980 b, 1981 b, 1983 c, 1987 b; etc.), while others have criticized them, sometimes severely (LAURENT, 1964: 145-146; 1972: 5-7, 26-28; 1973; KLUGE, 1966; DUELLMAN, 1977). What seems to have escaped some of these contradictors is the fact that INGER, contrary e.g. to ILLIES (1970) (see below), has not in the least proposed an " ecological concept of the genus " (LAURENT, 1972: 26), but has simply proposed to take into account, when this is possible, the *additional* information that ecology may give. It is quite obvious that no classification can be based on the ecology *alone*, because of the vast body of convergences which punctuate biological evolution! As for the fact, which is sometimes invoked, that this criterion cannot always be used, because it is not always possible to know the ecology of the species, nothing is more true, but, as for other criteria discussed above or for the hybridizability criterion which will be discussed below, this does not preclude one from using it when it is possible! At any rate the existence of an ecological gap between genera generally implies that of a morphological gap, and the morphological characters involved are generally complex (INGER, 1958).

As we shall see below, some criteria, and in particular the new hybridizability criterion, can be used only to *group together* species within a same genus, never to break up a genus. The ecological criterion, on the other hand, may be particularly useful, precisely when the data on hybridization do not contradict it, for *separating* into distinct genera species which are morphologically close: it is the case for example for the amphibians genera *Rana* and *Amolops* (INGER, 1954, 1966), or *Bufo* and *Ansonia* (INGER, 1954, 1958). This criterion is less useful for grouping species together, since it may be as easy to demonstrate the existence of important ecological differences between species as it may be difficult, unless their ecology is particularly well known, to be certain that there exists no significant differences between two species in such or such domain of their ecology.

Source : MNHN, Paris

Source : MNHN, Paris

THE PROBLEM OF GENETIC SIMILARITY

The history of life on earth is the history of organisms, of their cells, and of of the appearance, the transmission and the evolution of the DNA molecule. It is therefore a unitary process, but not for all that a continuum: DNA can usually be exchanged, recombined, only between organisms which are "close" enough. Discontinuities do exist, which allow the subdivision of the world of living beings.

In this respect, the species is a well-defined genetic unit: it is a closed gene pool, more or less protected from other similar pools (see e.g. Bocquet, Génermont & Lamotte, 1976, 1977, 1980). The genus, which groups together such units which are disjunct in nature, cannot be defined in the same way. Is it possible however to combine in a genus species having "close" genotypes, because they derive from a same ancestor? This will be possible if we have a way of estimating the genetic similarity between species. Several methods may be thought of for obtaining such an estimate: we shall examine them successively.

Genetic "distances" and "similarities"

To estimate the genetic resemblance between species, one might first think of making use of the various measurements of genetic "distances" and "similarities" which have recently developed. Most of these methods are based on direct or indirect comparisons of the molecule of a given protein such as it exists in several species: indirect methods are based on electrophoretic or immunological techniques, while direct methods, heavier and more costly and therefore still much less used, are based on the reconstruction of the primary structure of proteins (for a presentation of these methods and of the results they permit, see e.g. Ayala, 1977).

The methods of measurement of genetic distance based on proteins are of great interest because they give us valuable information for the reconstruction of the phylogeny of a given group. As a matter of fact recent works indicate that, at least for many proteins, the appearance of differences between homologous molecules of different species deriving from common ancestors happens at a relatively constant rate for a given protein and within a given group. This rate is a function of the time elapsed since the separation of the two lineages, and is independent from the rate of morphological evolution, as well as from the speciation rate, in these lineages. These phenomena are still the subject of a lively discussion among biochemists, but it seems well established that we now dispose of a *molecular clock of evolution* (Zuckerkandl & Pauling, 1962; Wilson, Carlson & White, 1977): provided some methodological precautions are taken, it is possible, within a given group, to have at least an approximate idea of the time elapsed since the separation of two lineages which have led to two living species, simply by measuring, by one of the methods evoked above (and in particular those, of more generalized use, which are based on protein electrophoreses or on immunological techniques),

Source : MNHN, Paris

the genetic distance between these species. This genetic distance is of great interest in studies of phylogeny, inasmuch as it allows the construction of hypotheses on the dates of cladogeneses, and also the detection of certain morphological convergences (see e.g.: MAXSON & WILSON, 1974; MAXSON, 1977).

Such methods allow us therefore to have an idea of the age of the lineages of which we nowadays observe the descendants. To classify the animals according to the similarity of their proteins would therefore largely come down to classifying them according to the greater or smaller age of their common ancestor: such a criterion would be acceptable from a cladistic point of view, but it is not so for the synthetists, who aim at expressing in the classification, not only the properly cladogenetic aspects of evolution, but also its anagenetic aspects, and therefore at taking into account the greater or lower holomorphological divergence which may have occurred in the various lineages after the cladogeneses which have separated them.

But would it not be possible to obtain a more trustworthy measure of the genetic similarity of organisms by directly comparing their DNAs? Such direct comparisons, on a large scale, raise of course important technical problems, but it is now possible to tackle this problem through the study of DNA hybridization: the quantitative measurement of the success of this hybridization indicates the degree of similarity of the chains compared (see e.g.: HOYER, MCCARTHY & BOLTON, 1964; AYALA, 1977; SIBLEY & AHLQUIST, 1982; DIAMOND, 1983). Furthermore it seems that, in a rather close future, the direct comparison of the structure of portions of DNA chains will be possible, thanks to recent methods which allow drawing up gene sequences (ABELSON, 1980). The data currently available on comparisons of DNA in different species are still not numerous, but they seem to indicate that the measurements thus obtained are much better correlated with those derived from the comparisons of proteins, therefore with the time elapsed since the separation of lineages, than with the holomorphological divergence which has occurred during this period between the lineages in question (WILSON, MAXSON & SARICH, 1974; SIBLEY & AHLQUIST, 1982). The DNAs of two given species are however appreciably more different than their proteins, probably because of the redundancy of the genetic code or of the existence of differences in the non transcribed regions of the DNA chain (KING & WILSON, 1975). Despite these differences, we are more or less brought back to the preceding problem.

It is interesting to note that even before the existence of methods allowing the comparison of the DNAs of different species, some authors had had the perceptiveness to foresee that the knowledge, even complete, of the structure of the DNA of species would be, although certainly very useful, insufficient in itself to build up a classification of animals, contrary to what other authors believed then (e.g. SIBLEY, 1962) or still believe (e.g. SIBLEY & AHLQUIST, 1982). Thus SIMPSON (1962: 502) wrote:

> " SIBLEY (1962), agreeing with some others, has suggested that the ultimate (*i.e.*, the touchstone?) for classification would be the complete DNA code. Certainly I can think of nothing more desirable as an *addition* to our criteria for classification, but I strongly doubt whether even that most desirable of criteria would be sufficient in itself. At high taxonomic levels, particularly, I suspect that interpretation of DNA resemblances and differences would be as difficult as interpretation of anatomical resemblances and differences and that the two would have to be combined, with each other and with all other classes of data, for the soundest result. "

SIBLEY (1965: 120) then implicitly admitted the validity of this criticism by writing:

> " Finally, let it be clearly understood that the application of the methods of molecular biology to systematics does not insure the solution of all of our problems. The new techniques provide new kinds of calipers which can measure previously unavailable characters but the interpretation of the data still requires a systematist who knows, appreciates and understands the other available information about the group of organisms he is studying. The molecular data are enormously exciting, and hold great promise for

Source : MNHN, Paris

future discoveries, but they must be viewed as additions to, not substitutes for, what is already known about the genetic relationships and evolutionary history of plants and animals. "

In the same spirit, MOORE (1967: 466-467) underlined that the number of different alleles between two species was insufficient to measure the genetic divergence between them:

" One has to know the consequences of the genic action. A few allelic differences might result in two profoundly different populations; a greater number of allelic differences might result in only trivial differences.
There is no way at the moment to compare the complete genotypes of different individuals, but this may soon become possible with the improvement of techniques for the hybridization of DNA's of diverse origins. This method will be subject to the important restriction mentioned above, namely that all genes are not equal in their effects. "

For his part, MAYR (1970: 321-322) wrote:

" Indeed, it is becoming increasingly evident that an approach that merely counts the number of gene differences is meaningless, if not misleading. (...) Nor can species difference be expressed in terms of the genetic bits of information, the nucleotide pairs of the DNA. That would be quite as absurd as trying to express the difference between the Bible and DANTE's *Divina Commedia* in terms of the difference in the frequency of the letters of the alphabet used in the two works. The meaningful level of integration is well above that of the basic code of information, the nucleotide pairs. "

LEWONTIN (1974: 20) expressed similar ideas in different words:

" To concentrate only on genetic change, without attempting to relate it to the kinds of physiological, morphogenetic, and behavioral evolution that are manifest in the fossil record and in the diversity of extant organisms and communities, is to forget entirely what it is we are trying to explain in the first place ".

Finally STANLEY (1979: 56) also defended this viewpoint:

" Genomic components have significance only in terms of phenotypic expression. A bear probably has been transformed into a panda by a few genetic alterations, but the result is an enormous amount of adaptative change, not a little. The notion that rates of evolution ideally should be measured by genomic rather than by morphological parameters (...) excludes from consideration the phenotype, upon which selection operates. We desire to understand the genetic mechanism of major evolutionary transformations of the sort that occurred in the origin of the giant panda, but the kinds of genetic information to be sought can be gleaned only through study of phenotypic change. "

If I deemed necessary to produce these various quotes, it is because, despite these few stands, many authors are still not conscious of these problems, and one still much too often finds publications where the " genetic distance " based on proteins is considered a good measure of the overall genetic resemblance between the species compared, which is obviously wrong.

The large discrepancy which exists between the morphological and molecular resemblances between species (WILSON, CARLSON & WHITE, 1977; CHERRY, CASE & WILSON, 1978) has been largely realized only in the last years. It poses interesting problems which we shall discuss again below, but let us note from now on that there would be no question of attributing *automat-*

Source : MNHN, Paris

ically a given systematic rank to groups of species having between them a given divergence at the molecular level, as it has been contemplated and even put into practice by some authors (e.g.: WALLACE, KING & WILSON, 1973; MAXSON & WILSON, 1975; LANZA, CEI & CRESPO, 1976; MAXSON, 1976; SIBLEY & AHLQUIST, 1982; see DIAMOND, 1983, for a series of references on " taxinomy by nucleotides "): this would eliminate a whole aspect of evolution, morphological, ecological and other divergences, which may be more or less important and more or less rapid between genealogically closely related species. The fact that human polypeptidic chains are more than 99 % identical to those of chimpanzee (KING & WILSON, 1975), which corresponds to the difference which exists, in other groups of organisms, between dualspecies (see BERNARDI, 1980, for the use of this term rather than that of " sibling species "), is of great interest for it expresses the fact that hominid evolution has been particularly rapid. It does not imply at all, however, the need for abandoning classifying man and chimpanzee in two distinct families.

STRUCTURAL GENES AND REGULATORY GENES

Despite their high technical foundations, the measures of genetic similarity that we discussed above give us only a static and distorted idea of the resemblances between two genotypes. As a matter of fact, they inform us about the purely *structural* resemblances between these genotypes, but scarcely on their *functional* resemblances. The genotype is not a *sum* of genes simply placed side by side. It is an *integrated whole* of genes which interact together (MAYR, 1975, 1982 b). The fundamental biological properties of an organism are the result of these interactions, and not an addition of isolated genic activities. Therefore if we want to estimate, not only the phylogenetic kinship of the species as allowed by the molecular methods mentioned above, but the whole similarity of genotypes, as *functional units*, we will need a *weighted* method of measurement, which takes into account the fact that all genes do not play the same rôle, do not have the same importance, in the building up and the functioning of an organism, in other words a method based on properly biological criteria, and not only biochemical or molecular ones.

The first method which comes to mind in this respect is that of phenetic comparisons. As a matter of fact it is certain that, up to a certain point, morphological resemblance expresses in a synthetic way the similarity of genotypes, and that a classification based on phenetic comparisons alone is generally a very good starting point for any synthetic classification (MAYR, 1981). However, as we have seen, this resemblance may be misleading (convergence, parallèlism), and on the other hand it may not be at all correlated with molecular data, i.e. with a measure which is apparently more precise, finer, of the genetic characteristics of the forms compared. How can we solve this contradiction?

We must here turn to recent developments of genetics, which point to the long ignored importance of regulatory genes, both during the ontogenesis of a given individual and during the evolution of living beings. Without going into the details, for which I refer the reader to the reviews by ZUCKERKANDL (1976 a, 1976 b), WILSON, CARLSON & WHITE (1977) and RAFF & KAUFMAN (1983), I shall mention some results of this research which are particularly important as regards the problem that concerns us here.

Let us first recall the fundamental distinction between two types of genes:

— *structural genes* code for messenger RNAs which are themselves translated into polypeptids; a mutation in one of these genes entails often (but not always, because of the degenerated nature of the genetic code) a modification of the primary structure of the polypeptid synthesized; such modifications are detected by the methods of comparison of proteins mentioned above;

— the rôle of *regulatory genes* is the regulation of the expression of structural genes: according to the cell and to the moment, they induce certain genes to be active, they inhibit others, etc.; a mutation in one of these genes may induce

Source : MNHN, Paris

a modification of the activity of many other genes.

The distinction between structural and regulatory genes was first established experimentally by JACOB & MONOD (1961) in Bacteria. Later on, the existence of regulatory genes was also demonstrated in Eucaryotes: these genes are situated in the " noncoding " parts of the DNA, which are of several types and occupy an important proportion of the DNA of Eucaryotes (see e.g.: WALKER, 1979; RAFF & KAUFMAN, 1983). The definition of regulatory genes given above may appear vague, but it is difficult at the moment to be more precise:

> " Considering the complexity of regulation and how little we know of its details, it may be foolish to even attempt to define a regulatory gene. Nevertheless, it is important to have at least a working definition if we are to study the evolution of regulatory genes and their role in adaptation. Thus, let us define a regulatory gene as any gene that directly affects the amount, the tissue distribution, or the developmental profile of another gene product. This working definition tells us, if nothing else, what kinds of phenotypes might result from genetic changes at regulatory loci, namely (a) differences in the levels of a structural gene product in some or all of the tissues of an organism (quantity variants), (b) differences in the presence or absence of the structural gene product in different tissues of the organism (tissue variants), and (c) differences in the time of appearance during development of the structural gene product (temporal variants). It should be clear that these need not be mutually exclusive categories of regulatory gene variants. In fact, in most cases (see below) there is substantial overlap in the phenotypes, e.g., a particular strain may have an elevated level of a structural gene product because that gene becomes active earlier in development. " (MACINTYRE, 1982: 265-266).

The processes of genetic regulation in Eucaryotes are obviously very complex, and if models have already been proposed in an attempt to describe them (ZUCKERKANDL, 1964, 1976 a; BRITTEN & DAVIDSON, 1969; DAVIDSON & BRITTEN, 1973; WHITT, PHILIPP & CHILDERS , 1977; RAFF & KAUFMAN, 1983; etc.), those remain probably still oversimplifications of the reality. Despite the still very preliminary stage of research on genetic regulation in Eucaryotes, it is interesting to look into the results already obtained.

The first important result of recent research is the discovery that the evolution of regulatory genes and that of structural genes are largely independent from one another. As we have seen, the evolution of structural genes is relatively regular: for a given gene and within a given systematic group, it seems to be simply proportional to time or almost so. On the other hand, the evolution of regulatory genes does not at all seem to exhibit the relative regularity of that of structural genes. It seems that in certain groups (the " living fossils ") these genes have not evolved during hundreds of millions of years — or hardly at all — while in others (e.g. hominids) they evolved very quickly.

The disparity in the evolution rates of both types of genes was well put in evidence in vertebrates by Allan C. WILSON's team in Berkeley. Thus the evolution rate of albumin seems to have been roughly identical in anuran amphibians and placental mammals, while morphological evolution has been slow and weak in the first group and rapid and important in the second (WALLACE, MAXSON & WILSON, 1971; WALLACE, KING & WILSON, 1973; WILSON, SARICH & MAXSON, 1974; MAXSON & WILSON, 1975; CHERRY, CASE & WILSON, 1978; CHERRY *et al.*, 1979, 1982). According to these authors, the evolution of phenotypes would be correlated more to the evolution of the systems of genetic regulation than to that of structural genes. This would explain the fact that morphological divergence is largely independent from molecular divergence measured at the level of structural genes of proteins. Both phenomena express different aspects of the genotype and, from the viewpoint of evolution, morphological divergence is much more important a synthetic indicator than divergence at the level of protein molecules. The latter may be a simple, more or less exact, function of time, while morphological

Source : MNHN, Paris

modifications take place at variable speeds and are linked to the history of the group, and in particular to the history of its adaptations.

It is therefore not unreasonable to think that it is the evolution of the systems of genetic regulation which accounts for the major part of the morphological evolution of organisms. New types of structures, of organs or of organisms may appear following modifications in the systems of genetic regulation, but often without the appearance of noticeable differences at the level of structural genes.

As we have seen, polypeptidic chains and DNAs of man and chimpanzee are more than 99 % identical (KING & WILSON, 1975), although these two species are extremely different in their morphology, development, behavioral capacities, etc. The differences between these two species would be accounted for by differences in their systems of genetic regulation.

Thus, the results of recent research on the molecular aspects of evolution throw new light on the already ancient conceptions, which may be found e.g. in the works by J. S. HUXLEY, G. G. SIMPSON or E. MAYR, on the existence of different rates of anagenesis at different epochs and in different lineages: these different rates of anagenesis could correspond to different rates of evolution of regulatory genes.

The construction of a weighed, synthetic index of genetic similarity is therefore not an easy task. Quite rigorously, such an index should take into account the five following distinct types of similarity (ZUCKERKANDL, 1980): (1) *structural* similarity of the genes (functional units of the DNA) and of the DNA as a whole; (2) *functional* similarity of the direct (RNA) and indirect (proteins) products of the genes; (3) similarity of the *types of interactions* between genes, in different tissues and at different moments; (4) similarity of the *quantitative aspects* of these interactions; (5) similarity of the *results*, at the various supramolecular levels, of these interactions.

These factors are still far from having all been analyzed and, furthermore, we still do not have a method which would allow an *integration* of the results of the analyses made at these different levels so as to obtain a single global index of similarity. A rigorous synthetic measure of the genetic similarity of two organisms is therefore impossible at the moment, but some elements do exist for such a measure.

First of all, as we have seen, biochemical techniques allow us now to obtain a direct or indirect measure of the structural similarity of genotypes, (1) above: percentage of genes, or even of triplets, that two organisms have in common (which are identical in both). This similarity is usually indirectly estimated by the " genetic distance ".

On the other hand, the similarity of results, (5) above, is largely measured by phenetic methods. The analysis must bear on the holomorph, and not be limited to the morphology alone.

But these data are still insufficient: they do not allow one to measure the functional similarity of genotypes (similarity of the systems of genetic regulation which govern the expression of the structural genes, (2) to (4) above).

In particular it must be underlined that *all genes are not active in the adult* and that a measure of genetic similarity between species which would only be based on the characters of adults would be largely biased. During ontogeny (embryogenesis and growth), many genes, which were inactive in the egg and which will be so again in the adult, become successively active. In other words, during development, modifications occur in the types of interactions between genes and the quantitative aspects of these interactions, (3) and (4) above, and these modifications are important to take into account in any analysis of genetic similarity.

The species with castes, the animals with metamorphoses and even more so the parasites with cycles, give a good illustration of the various potentialities of a genotype which are revealed only successively or alternatively. Thus for example, in the Digeneous Trematoda, miracidium, sporocyst, redia, cercaria, metacercaria, adult, are successive stages which make evident the importance of the rôle of the systems of regulation in the expression or the inhibition, at various stages of the life of an animal, of the various morphogenetic potentialities present in its genotype.

Thus in order to be able to take into account, in the classification of animals, the genetic resemblance between species, one must not content oneself with the " classical " methods of measurement of " genetic " distances, but one must also possess a method of estimation of the functional similarity of genotypes. Until now, a

Source : MNHN, Paris

single, indirect, method, has largely been used by systematists in this aim: the measure of overall morphological resemblance between species. I suggest here that a second synthetic method of measurement of the functional genetic resemblance, which until now has been only very little used by systematists, could be taken advantage of: it is the study of a natural or artificial experiment, that of *interspecific hybridization*.

Hybridization and genetic similarity

The hybridization of *individuals* (and not of their cells, of their DNAs or other molecules) is a *synthetic* indicator which has often been neglected but which may be very useful to appreciate the *degree of biological* (and not biochemical) *compatibility* of two genomes, *in an organism and to build an organism*, and to measure their degree of *functional* (and not only structural) *resemblance*. The fact that two genomes may "agree together" and succeed, together, in "building up" an organism, indicates that, not only their structural genes are similar or at least compatible, but also that their systems of genetic regulation are compatible (Wilson, Maxson & Sarich, 1974; Oliver, 1979). This is an indication of a very high functional genetic similarity.

What is particularly significant in this criterion is that it appeals to the ontogeny of the organism, and therefore that it takes into account, among others, all the genes which become active only during a period, sometimes very short, of development, and are inactive in the adult.

The difference between the hybridization of individuals and that of cells must be underlined. Cell hybridization consists in the putting together, in a cell culture, within a single cell, chromosomes of two different species. Such cell hybrids may be obtained between extremely distant species, such for example as man and the mosquito *Aedes aegypti* (Zepp *et al.*, 1971). These hybrid cells live and divide during several generations, for they are not obliged to develop and build up an organism. It is likely that few genes are active in these cells as compared with the number of genes which take part in the whole ontogeny of an organism.

On the other hand the hybridization of individuals generally succeeds only between species which are considered, after all other biological criteria, as relatively close or very close to each other. From the zygote until the adult, these hybrid organisms are able to activate, one after another and in a coordinate way, their various genes and systems of genetic regulation without provoking a lethality. This is a very strong indication that both species are closely related and have a high overall genetic similarity.

Classical hybridization (crossing of two individuals and obtaining of one or several hybrid zygotes) is not the only method allowing a measurement of this genetic compatibility between species. Other more recent methods should produce interesting data in this field. The most important of these methods, discussed in detail elsewhere (Baltzer, 1952; Fankhauser, 1955; Moore, 1955; Brachet, 1957; Briggs & King, 1959; Chen, 1967; C. L. Gallien, 1970; L. Gallien, 1972; Subtelny, 1974; Danielli & Diberardino, 1979; Diberardino, 1980), are the following ones:

— production of haploid hybrids: after fertilization of the ovum of species A by a spermatozoon of species B, and before amphimixy, the female pronucleus is retired from the egg; the egg develops then with a cytoplasm A and a single set of chromosomes B; in amphibians, Moore (1967) has shown that this system is more sensitive than normal hybridization to detect genetic incompatibilities between species;

— doubling of the paternal stock of chromosomes in the egg of the previous experiment: this egg then develops with a double stock of chromosomes B in a cytoplam A;

— production of polyploid hybrids, e.g. by fertilizing a diploid ovum A with a spermatozoon B; various other combinations are also possible, which allow a fine study of the developmental consequences of the presence of different doses of chromosomes of the two parental species in the egg;

— nuclear transplantation: a diploid nucleus

Source : MNHN, Paris

of a species B is introduced in an enucleated egg of species A;

— injection of cytoplasm of a species B into the egg of a species A or into a hybrid egg: it is then possible to study the effect on the development of different cytoplasmic, and not chromosomal, doses (Ansevin & Williams, 1974; Aimar & Delarue, 1976; Aimar, 1977; Delarue, 1977 a, 1977 b; Aimar, Delarue & Vilain, 1981);

— graft of lethal hybrid tissues on viable embryos: this allows one to determine if the lethality of these hybrids is due to factors present in all the tissue of the hybrid, or on the contrary present in certain tissues only, from which for example toxic substances may diffuse in the whole embryo and provoke its death;

— *in vitro* culture of hybrid tissues or cells.

All these techniques are extremely interesting. Unfortunately they have only been used until now on a small scale in experimental works of developmental biology bearing on nucleo-cytoplasmic relationships and realized in limited groups of animals, mainly amphibians. They cannot therefore be the subject of generalized use in zoology as yet, and in what follows we shall only consider the results of classical hybridization. However, in order to interpret these results correctly and to be able to use them in systematics, we must first recall the different types of phenomena which have been observed during animal interspecific hybridization: this question is the subject of the next chapter.

Source : MNHN, Paris

A FEW GENERAL FACTS ABOUT ANIMAL HYBRIDIZATION

The mechanisms of interspecific isolation

Species are protected genetic pools, which keep their genetic identity thanks to the existence of factors or mechanisms of interspecific isolation. As a matter of fact it is important to distinguish between *biological mechanisms of isolation* proper, and *exogeneous factors of isolation*, for the latter are not determined by the genotype of the species but by external conditions, extraneous to the species themselves. As for the mechanisms of isolation, they are of two types: *pre-ejaculatory* and *post-ejaculatory* mechanisms.

Other names have been given to the last two categories, but they seem to me inadequate for the following reasons: the words pre-copulatory and post-copulatory do not apply to animals in which there exists no copulation in the strict sense of the term (Dubois, 1977 b); the words prereproductive and postreproductive, which are too imprecise, and the words prezygotic and postzygotic, which are more precise, are not adequate to designate these categories, because gametes of the individuals of both sexes may be emitted without this being followed by the formation of zygote(s). What is particularly important, in natural populations, is that male or female gametes be emitted or not, because if hybridization fails these gametes will have been wasted in vain; natural selection will thus act in the sense of reinforcing the mechanisms of isolation which intervene before the emission of gametes (Mecham, 1961; Watson & Martin, 1968; Littlejohn, 1969; Dubois, 1983 a). I propose the use of the term " ejaculation " as a general term designating the emission of gametes of both sexes, not only of male gametes: this is conform to the etymology, the Latin verb *ejaculare* meaning " to project with strength a liquid secreted by the organism ", not necessarily sperm. Furthermore, in many animal species, both types of gametes are emitted at the same time, at a given moment of the mating act, which may be designated as " ejaculatory ". In the classification of isolation mechanisms which follows, the major dichotomy is placed between pre- and post-ejaculatory mechanisms, rather than between pre- and post-zygotic mechanisms, which also exist but as subdivisions of the post-ejaculatory category.

Exogeneous factors of isolation

Geographical barriers

The individuals of two allopatric populations never have an occasion to meet, and hence there exists no material possibility of hybridization between them.

Temporal barriers

Similarly, individuals belonging to two allochronic populations have no possibility to hybridize: it is the case of fossil species from different periods of time, or in relation to contemporaneous species, but the scale of time considered may also be very short.

Source : MNHN, Paris

Biological mechanisms of isolation

Pre-ejaculatory mechanisms

They prevent mating and/or the emission of gametes of individuals of both species.

Ecological mechanisms

They may be *spatial* (both species having different habitats or reproduction sites), *temporal* (both species having different periods of activity or of reproduction, be it different seasons or different periods in the nycthemerous), or both. In this case, animals of both species do not meet, at least not during their reproduction.

Behavioural mechanisms

The animals of both species may meet, but not breed together, for one of the following reasons:

— total absence of attractiveness of the animals of both species one for another;

— the animals of one sex (generally the males) of one species are attracted by those of the other sex of the other species, but the later repulse them and refuse to mate;

— the animals of both sexes are attracted, the preliminaries to breeding start, but do not go to their end because of the existence of too important differences between the nuptial parades or other characteristics (morphology, colors, etc.) of both species.

Among the behavioural mechanisms of isolation, the following ones may be cited, according to the physical sense on which they call:

— those which involve hearing: specificity of the mating calls;

— those which involve sight: specificity of the colors, of the shape, of the size and of other visible morphological characters; specificity of the behaviours in sexual parade;

— those which involve touch: specificity of the shape, of the size, of the texture, of the movement;

— those which involve chemical senses: specificity of the sexual pheromones or of other chemical stimuli.

Mechanical mechanisms

In this case mating begins but does not lead to the emission of gametes, for the copulatory organs of both species are not compatible and do not allow a complete copulation. Size in itself may be a factor of mechanical isolation: a male and a female with too dissimilar sizes do not always succeed in mating, even in the absence of behavioral mechanisms of isolation between them.

Post-ejaculatory mechanisms

These mechanisms act after the emission of gametes. The classification which follows is based on the results of the numerous works devoted to interspecific hybridization in various groups of animals, and in particular of echinoderms, insects, teleosts and amphibians (Montalenti, 1938; Moore, 1955; Stebbins, 1958; Cousin, 1967; Blair, 1972 b; etc.).

Prezygotic mechanisms

In this case the emission of gametes of both sexes, or at least of male gametes, takes place, but these die before coming into contact, or come into contact but without leading to a true fertilization. Several distinct situations may be met with in this category:

— Absence of attraction of sperm for ova: this case may occur in aquatic animals in which gametes are directly emitted in water without copulation.

— Destruction or immobilization of sperm in the female genital tract, in particular following an antigenic reaction of female towards them.

— Inability of sperm to go through the jelly of the ovum, either because they are stopped or killed by the jelly, or because in the later some factors are lacking which are essential for the

Source : MNHN, Paris

penetration of the spermatozoon in the ovum itself (see ELINSON, 1974).

— The spermatozoon does not enter the ovum but leads to its activation, and sometimes to its development by *gynogenesis*; this may give birth to *false hybrids* which are usually haploid and sometimes diploid (in the case where the ovum was diploid or when a doubling of the maternal stock of chromosomes has occurred after activation and before the first division of the egg).

— The spermatozoon enters the egg but amphimixy does not occur. Paternal chromatin does not differentiate in chromosomes, it degenerates and is later destroyed or expulsed from the egg, which may however sometimes develop and give birth to a false hybrid.

Postzygotic mechanisms

These mechanisms only act when there exists a true zygote, i.e when fertilization has been complete and when amphimixy (karyogamy) has taken place between the male and female pronuclei. In the hybridization experiments which have been realized in the whole animal kingdom, all intermediates have been observed between amphimixy followed by no development and obtention of adult hybrids, fertile and normal in all:

— Amphimixy followed by no development.

— Amphimixy followed by the subsequent, early or late, total or partial, elimination of paternal chromatin. Here again, development may take place with the maternal stock of chromosomes alone (which gives birth to another type of false-hybrid), or with the maternal stock and a part of the paternal stock (which gives birth to an aneuploid hybrid or " partial hybrid ").

— Amphimixy followed by the development of the diploid hybrid zygote. In amphibians, the following different cases can further be distinguished:

- Development till the end of the blastula stage, the embryo proving unable to realize gastrulation.
- Arrest of development during a subsequent embryonic stage: gastrulation, neurulation, tail bud stage.
- Hatching takes place, but the larvae are abnormal (oedemas, microcephaly, etc.), do not feed and die.
- The larvae are apparently normal, they feed and grow but die after a certain time.
- Inability to get over the hurdle of metamorphosis.
- Metamorphosis takes place but the young amphibians are abnormal and die very soon.
- In the other cases, the animals which have gone through metamorphosis generally reach the adult stage. Several cases are still possible:
  * The adults are viable but present various somatic anomalies which may interfere with their survival or their reproduction.
  * The adults of both sexes are unequally represented (inbalance of the sex-ratio), and sometimes even one sex may be completely absent.
  * The adults of both sexes are not fertile.
  * The adults of one sex are not fertile.
  * The adults are fertile but their F2 or backcross progeny exhibits some of the anomalies described above for the F1: arrest of development at a given stage, anomalies, infertility.
  * The adults are viable and fertile but show a repression of their genic activity at certain loci.
  * Finally, the adults are viable, fertile and fully normal, and their progeny itself is normal.

A few other types of post-ejaculatory postzygotic mechanisms of isolation also exist, which do not involve mechanisms internal to the zygote or to the embryo, but factors external to it. Two of them may be mentioned:

— The hybrid embryo may die at the stage of hatching, e.g. because it is unable to get out of the jelly of the egg (ELINSON, 1974).

— In viviparous animals, in particular mammals, the mother may develop an antigenic reaction against its embryos and synthesize antibodies against them, which cause abortion (see e.g. MEDAWAR, 1953; BILLINGTON, JAMES & KIRBY, 1968; KERR, 1968; CLARKE & HETHERINGTON, 1972; MAXSON, SARICH & WILSON, 1973; WILSON, MAXSON & SARICH, 1974; GUTTMAN, 1985).

Source : MNHN, Paris

SOME GENERAL RULES DRAWN FROM THE STUDY OF HYBRIDS

The study of artificial hybridization in animals, in particular in insects, echinoderms and amphibians, has allowed a certain number of general rules to be drawn (MONTALENTI, 1938; MOORE, 1955; STEBBINS, 1958; COUSIN, 1967; BLAIR, 1972 b; etc.). We will only mention here a few of them, those which have a particular interest for the systematist who desires to take advantage of hybridization facts for the establishment of a supraspecific classification of animals.

VARIABILITY OF RESULTS WITHIN A GIVEN TYPE OF CROSS

In a same type of cross (e.g. between the male of a species A and the female of a species B), it is frequent that the results of different experimental series show between them significant differences. Depending on the cases, these differences may be attributed to geographical variations in the genetic characteristics of the species crossed (animals of a single species but coming from distant regions of the distribution area of the species, or even from different populations in a same region), or simply to individual genetic differences (different animals from a same population). Such a variability can also be found in the vast majority of biological phenomena and has therefore nothing to surprise us, but it must be taken into account in the interpretation of results: it is very important, in this domain like in all others in biology, not to content oneself with a unique observation, but to multiply as much as possible the observations, therefore here the crosses, of the same type.

In natural and artificial crosses there exist numerous possibilities of an exogenous disruption of fertilization and of the development of hybrids. In many cases the failure of development of hybrids is due to such artefacts. It is one of the reasons why negative results of hybridization must always be accepted with some reservation.

BLAIR (1972 b) and his coworkers carried out a very wide survey of interspecific hybridization within a cosmopolitan genus of anuran amphibians, the genus *Bufo* (true toads). They made hundreds of crosses and reared thousands of hybrids. They were thus able to observe this variability of results for a single type of cross. BLAIR (1972 b) considers that an important part of the failures of development may be attributed to the difficulties of rearing, to diseases and other artefacts. For this reason, for a given type of cross the result which BLAIR (1972 b) takes into account for subsequent analyses is not the *mean* of the observed results, nor even the extremes, but the *best result* observed.

In reality, the variability of results is not only due to the artefacts introduced by man, but also to the genetic variability proper to species, populations and individuals; it is however difficult, not to say impossible, to take both kinds of variability into account. Furthermore, as we shall see, the failure of development may be caused by very simple and little significant genetic factors (a single gene may be enough), and has much less genetic, phylogenetic and taxinomic significance than the success of development of a hybrid. It is therefore justified to generalize BLAIR's (1972 b) method and to consider in what follows, for a given cross, only the best result observed.

Source : MNHN, Paris

Study of reciprocal crosses

One might think that the major if not unique factor which is responsible for the failure of development of hybrids is the fact that the paternal and maternal genomes do not succeed in working correctly together and to induce a normal development of the embryo. To be sure, the phenomenon exists, but another phenomenon plays an important part, from the start of development, in many cases of lethal hybridization: it is the incompatibility between the paternal chromosomes (which are brought by the nucleus of the spermatozoon) and the cytoplasm of the ovum.

The cytoplasm of the ovum has been synthesized during oogenesis, i.e. under the control of maternal genes alone. It contains in particular messenger RNAs which play an important rôle in the first stages of development. The paternal genes, or some of them, often prove incompatible with this cytoplam, which leads to a failure of development. This phenomenon has been well demonstrated by various methods, and it has been possible to show that the incompatibility between the ovum's cytoplasm and the paternal genes could be of several types (see in particular Stebbins, 1958). Without going into details, let us emphasize that the importance of this phenomenon appears very clearly in particular in the case of reciprocal crosses.

As a matter of fact, when two species A and B are crossed, the result is frequently different according to whether the cross has been made in the sense female A by male B or female B by male A. Sometimes only one of the two crosses gives birth to viable hybrids, sometimes only one gives birth to fertile animals, sometimes both give birth to animals the development of which stops at different stages, etc.

In both types of crosses the genetic material present in the zygote is the same: one set of chromosomes (and genes) A and one set of chromosomes (and genes) B. What differs is only the cytoplasm containing these chromosomes. The experiments show that the same hybrid genotype AB may be able to give a normal development in cytoplasm A, but unable to do so in a cytoplasm B (for the detailed analysis of a case of this type, see Elinson, 1981).

As we have seen, for the systematist the positive results of hybridization are more meaningful than the negative ones. In the cases where reciprocal crosses give different results, it will therefore be indicated again only to retain the " best result ", the result of the most successful of the two types of crosses.

The major stages of failure of hybridization

Despite the vast diversity of the stages of failure of development of hybrids that we mentioned above, some of these stages are more significant and more important than others to consider, for the developmental arrest occurs preferentially there. We shall insist here only on three of them, which are most frequent and general in the whole animal kingdom.

Arrest of development at the end of the blastula stage

In a great number of interspecific hybridizations, in particular in amphibians, development proceeds normally until the end of the blastula stage. When one looks closely into it, one may observe that it very much resembles the development of normal non hybrid eggs of the maternal species (if it shows any differences as compared with that of the paternal species). It has been possible to demonstrate by various methods that the segmentation of the amphibian egg until the end of the blastula stage is occurring without intervention of the egg nucleus, or with a very limited intervention of it. What is crucial is the egg cytoplasm: the segmentation is principally or entirely determined by the genic products transcribed during oogenesis from maternal genes and present as messenger RNAs in the cytoplasm of the ovum.

Source : MNHN, Paris

It is only at the beginning of gastrulation that the massive activation of the genes of the embryo nuclei begins, and therefore, in addition to the maternal genes, of the paternal genes. It is often at this moment that the incompatibility between both paternal and maternal genomes, or between the paternal genome and the maternal cytoplasm, expresses itself, and this is why an arrest of development is observed at this stage in many cases of animal hybridization, especially in amphibians.

The fact that two species may be able to give viable hybrids until the end of the blastula stage is therefore of little genetic or phylogenetic meaning and is of little interest to the systematist.

Arrest of development at an embryonic stage subsequent to the blastula stage

This arrest may take place during gastrulation, neurulation, or later. This phenomenon clearly expresses an incompatibility, either between the paternal and maternal genomes, or between the paternal genome and the hybrid cytoplasm, or still both phenomena together. However, in detail, the causes and modalities of the inviability of hybrids may be numerous (see in particular STEBBINS, 1958), and the failure of development at these stages is therefore difficult to interpret.

This failure may in some cases be due to a single lethal gene; this is very strikingly shown by the recent description of the gene *Lhr* (" Lethal hybrid rescue ") of *Drosophila simulans* (WATANABE, 1979; TAKAMURA & WATANABE, 1980). Since the discovery of this latter species (STURTEVANT, 1919, 1920), it has been known that the crosses between *Drosophila melanogaster* females and *Drosophila simulans* males only give birth to female hybrids, while the reciprocal crosses give only male hybrids, the development of the other sex being blocked during larval stages. However the hybrids of both sexes carrying the gene *Lhr* are viable in both types of crosses. This gene constitutes therefore in itself an efficient postzygotic mechanism of isolation between the two species of *Drosophila*, but, " apart from this gene ", these two species remain genetically very close, their genomes being compatible and able to induce together a normal development:

> " In the evolution of *melanogaster* and *simulans* into separate species there must have a stage in which the hybrids of both sexes were viable. Then, at a later stage the unisexual inviability that now characterizes the hybrids somehow arose. It is very likely, in view of the results reported in this paper, that this was a mutation from *Lhr* to *Lhr*⁺ and, if so, then the *Lhr* gene represents an evolutionary step backward. This encourages the search for other mutants which reverse the evolutionary process of reproductive isolation. " (WATANABE, 1979: 330-331).

If the inviability of hybrids is of unclear meaning, on the other hand the success of the development of hybrids expresses without ambiguity the absence of major incompatibility between the two genomes brought face to face and the cytoplasm, and has therefore a clear meaning, which we shall discuss again later.

In amphibians, experience has shown that in many cases, when the development of the hybrid has taken place in a harmonious or almost harmonious manner, until the stage of tailbud, then it goes on normally: developmental arrest at the stage of hatching, of larval development, of metamorphosis and of post-metamorphosis growth do exist, but they are rarer and probably less significant.

Infertility of hybrids

In many crosses, F1 hybrids become adult but prove then infertile, or give birth to non viable, abnormal or infertile progeny (F2 hybrids or backcrosses with one of the two parental species).

Here again, we won't go into details, but let us mention that the causes of this infertility, as numerous as they may be, all fundamentally express the same phenomenon as the non-viability of F1 hybrids: a disequilibrium, an incompatibility between the two parental genomes and/or between the paternal genome and the cytoplasm of the hybrid. Let us remember, however, that

Source : MNHN, Paris

two major types of hybrid sterility have been traditionally distinguished, genic (or developmental) sterility, due to an incompatibility between the genes of the two hybridized species, and chromosomal sterility, due to the existence of structural differences between the chromosomes of the two parents. Let us also remember that in many cases where the hybrids of a single sex prove non viable or sterile, they often, but not always, happen to belong to the heterogametic sex (HALDANE's 1922 rule). An excellent and detailed discussion of the problems related to the sterility of F1 or F2 hybrids and to the non-viability of F2 hybrids will be found in the work of STEBBINS (1958).

Therefore, the fact that an adult hybrid is infertile may be due to a number of causes. It is demonstrated that certain of these causes do not call upon numerous and complex genetic factors, and that sometimes, as for the non-viability of F1 hybrids, a single gene may be involved. In other cases, this infertility "simply" proceeds from the fact that the species crossed do not have the same degree of ploidy (e.g. in the cross between a diploid species and a tetraploid species derived from the first one): despite the very great similarity of the two species at the genic level, their hybrid, although perfectly viable until adult stage, is not fertile.

The infertility of hybrids having such an unclear meaning, it seems preferable not to take it into account in a work having taxinomic preoccupations.

GENIC EXPRESSION IN HYBRIDS

Rather recently, various works have been devoted to the study, by protein electrophoreses, of genic expression in insect and vertebrate hybrids (see the references given by DUBOIS, 1983 a: 51, and also: DICKINSON, 1980 a, 1980 b; PHILIPP, PARKER & WHITT, 1983; DICKINSON, ROWAN & BRENNAN, 1984; PASDAR, PHILIPP & WHITT, 1984; PASDAR *et al.*, 1984; PARKER, PHILIPP & WHITT, 1985 a, 1985b).

When two parental species have different and electrophoretically detectable alleles, it is possible to study in hybrids the expression of alleles coming from both parents. Several types of results may be observed:

— synchronous expression of both parental alleles: this is the most general result, which is obtained, at least for some genes, even in hybrids made between species deemed relatively distantly related by systematists, e.g. placed in different tribes (WHITT, CHILDERS & CHO, 1973);

— delayed expression of one of the alleles (generally the paternal one), which only becomes active at a later stage of development than the other allele;

— absence of expression of one of the alleles, which is said to be *repressed*: this is more often the paternal allele, more rarely the maternal allele and finally sometimes both alleles of a given gene.

A rather weak relation exists between the degree of allelic repression and taxinomic relationships between the species crossed. Thus in teleosts, WHITT, CHILDERS & CHO (1973) have observed that there exists usually no allelic repression between species of a same genus, and that the number of repressed alleles tends to increase with the systematic distance between species (belonging to different genera, different tribes, etc.). But exceptions to this "rule" also exist (see e.g. LUCOTTE & DUBOUCH, 1980).

Source : MNHN, Paris

Consequences as to the use of hybridization in systematics

What interests the systematist, in the study of hybridization, is the information that it may bring to him as to the *resemblance of the genomes* of both hybridized species. The measure of this genetic resemblance will be applicable to estimate the phylogenetic kinship of these species and their greater or smaller genetical divergence since their separation, and for the construction of a supraspecific classification.

Given this objective, it will be necessary, on one hand to try to eliminate as many as possible of the " parasitic " factors which interfere with hybridization, so as to leave only phenomena which can actually be explained by the structural and functional resemblances between the genomes of the two compared species, and on the other hand to dispose of methods allowing one to verify that what has been obtained are really true diploid hybrids between the two species.

Elimination of " parasitic " factors interfering with hybridization

Various types of methods can be called upon to try to eliminate these " parasitic " factors, according to the nature of these factors. Several cases may be distinguished:

— the case where the pre-ejaculatory factors and mechanisms of isolation between both species in nature are non-existing or imperfect: it will then be possible to study the eggs, larvae and adults in the zone where natural hybridization occurs;

— the case where the species are separated in nature by geographical barriers: the mere putting in contact, in captivity or in semi-captivity, of individuals of the two species separated in nature will sometimes be enough to obtain hybrids;

— the case where the species are separated in nature by ecological or behavioural mechanisms of isolation: their placing in captivity may be enough in certain cases to obtain hybrids (certain species which do not hybridize, even in sympatry, in nature, may do it in a cage or in an aquarium); in certain cases, an intervention of man is necessary to erase the behavioural barriers between both species, and this intervention may go as far as artificial insemination or fertilization;

— the case where mechanical or physiological barriers prevent fertilization, in particular in species with internal fertilization: one must then have recourse to artificial insemination or fertilization, sometimes after taking the ovum from the female genital tract, *in vitro* artificial fertilization and reimplantation of the egg in the female;

— the case of other more specific barriers; we will give two examples of these:

• In amphibians, some species never produce hybrids between themselves although they appear very close from all other viewpoints, or they may produce viable hybrids, which may sometimes become fertile adults, when the cross is made in one sense, but in the reciprocal cross the egg is never fertilized. In some of these cases, it has been possible to show that the failure of hybridization was to be ascribed to the jelly of the egg of one of the species, which stops the spermatozoon of the other one (Elinson, 1974, 1975 a, 1975 b; Brun & Kobel, 1977). When virgin ova of the species A, taken from the general cavity of a female of this species before they go through the oviduct, are placed in the general cavity of a female of species B which is laying its eggs, these ova go through the oviduct where they are covered with the jelly of this species. (This technique was invented and first applied by Rostand (1933), and for this reason I proposed (Dubois, 1982 a, 1983 a) to call it " Rostand's technique "). The ova are then liable to be

Source : MNHN, Paris

fertilized by sperm of the species B, and in some of these cases the development may then occur in totality and give rise to normal adults. According to ELINSON (1975 a), the fact that the jelly of the ova of *Rana clamitans* prevent the fertilization of the latter by *Rana catesbeiana* sperm could depend on two genes only, and the same probably applies to other similar cases. In all these cases, the genomes of the two species concerned may be very little different, and the few genes implied in the phenomenon of the block to fertilization in the jelly are, as concerns the problem of overall genetic compatibility of both genomes, artifacts, parasitic factors which must be disposed of: in a study of overall similarity between species, it will therefore be indicated in these cases to call upon ROSTAND's technique.

• In viviparous animals, the mother may develop an antigenic reaction against the hybrid foetus, which leads to abortion. This process is still imperfectly understood but here also such a reaction could well depend upon a small number of genes. It could be possible to avoid this artifact by making an *in vitro* culture of the hybrid embryo in order to follow its development in the absence of antibodies produced by the mother (see in this respect: MAXSON, SARICH & WILSON, 1973; WILSON, MAXSON & SARICH, 1974).

Despite their diversity, all the interventions that we have just mentioned are, with respect to the problem which concerns us here (resemblance of two genomes and their functional compatibility), of the same nature: they tend to suppress the factors which oppose the meeting of gametes of the two species considered, as well as all exogenous factors susceptible to oppose the development of the hybrid zygote.

DETECTION OF TRUE DIPLOID HYBRIDS

This being done, an additional precaution must be taken: it is necessary to ascertain that the animals produced by a cross are true *diploid hybrids* and not haploid or diploid "false-hybrids" (eggs developed by gynogenesis or having expulsed the paternal chromatin), aneuploid "partial hybrids" (a part of the paternal stock of chromosomes having been eliminated at the beginning of development), or even triploid hybrids (having e.g. two maternal and one paternal chromosomes sets). Such anomalies have been observed by BOGART (1972) among the numerous products of the crosses realized by BLAIR (1972 b) and his coworkers in the genus *Bufo*: in this case, the major cause seems to be that *Bufo* females often produce a low percentage of diploid ova, which may develop by gynogenesis or be fertilized and give rise to triploid embryos, but other mechanisms may be responsible for similar anomalies in other cases.

As was stressed by BOGART (1972), there is good reason for being particularly vigilant when the number of viable hybrids obtained is low, for example when, in a cross of amphibians implying hundreds or thousands of eggs, the number of eggs giving birth to larvae is very reduced as compared to the number of fertilized eggs: these larvae often prove to be gynogenetic or triploid. However they exhibit a normal morphology and cannot be detected as such by the sole examination of their phenotype.

Because of these problems, verification would be indicated in all cases where the progeny obtained is composed of real diploid hybrids by doing the following analyses:

— karyotype of the hybrid, allowing one to ascertain that it is diploid (or, more precisely, that it has a number of chromosomes equal to the sum of the haploid chromosomal numbers of the two hybridized species, which may be different);

— examination of the external phenotype (morphology, colors), permitting the discovery in some cases of the existence of a mixture of paternal and maternal characters;

— when this examination gives doubtful results, recourse to electrophoretic methods to see if an expression of both paternal and maternal alleles can be observed, at least at some loci.

Source : MNHN, Paris

INTERSPECIFIC HYBRIDIZATION AND SUPRASPECIFIC CLASSIFICATION

This chapter shall be devoted to a study of the relationships between the data of hybridization and the other types of data available concerning the species.

VARIABILITY OF THE RESULTS WITHIN A TAXINOMIC GROUP

This variability has long been emphasized by students of hybridization. If one considers a traditional taxinomic group, e.g. a genus of amphibians, the rule is that the results of interspecific hybridization are most varied, according to the species of this genus crossed two by two, from total failure or fertilization to complete development of normal hybrids. Furthermore there often exists no transitivity in the results: e.g. the species A and B give between them viable hybrids, B and C also, but the hybridization between A and C leads to a failure.

These results caused the authors to be prudent, if not suspicious, as to the use of the results of hybridization to estimate taxinomic relationships between species. In reality this suspicion is only partly justified. In my opinion, it is based on a methodological error: the one which consists in giving as much importance and meaning, in the genetic and phylogenetic interpretation of the results of hybridization, to the negative results as to the positive ones. For the reasons expressed above, positive results alone have a clear meaning in this field, and furthermore among these results it is preferable to take into account only the best results obtained. If this important distinction is made, the results of hybridization prove much less "anarchical" from a taxinomic point of view and may give us very useful indications.

HYBRIDIZATION AND MOLECULAR DIVERGENCE BETWEEN SPECIES

The functional genetic similarity measured by the synthetic criterion of hybridization does not coincide with structural genetic similarity measured by "genetic" distance, as was shown e.g. by AVISE & SMITH (1974) in Centrarchidae, or by Allan C. WILSON and his coworkers in various groups of vertebrates. With the help of immunological methods, these later workers have estimated the molecular divergence, at the level of molecules of albumine and of transferrine, between species of anuran amphibians, of birds and of placental mammals (see in particular: MAXSON, SARICH & WILSON, 1973; WILSON, MAXSON & SARICH, 1974; PRAGER & WILSON, 1975). Relying on the data concerning the "evolutionary molecular clock" (see above), these authors have deduced the presumed dates of the cladogenesis which has separated both lineages which have led to the two species now being compared. Furthermore they have taken into account the aptitude of these species to give viable hybrids between them. The results of these works are presented in table I, which also gives the mean number of species per genus in the concerned groups.

If we consider, following the arguments presented above, that the aptitude to give hybrids is the clue to a strong functional genetic similarity, one must admit that the genetic evolution of birds and of amphibians has been similar and

Source : MNHN, Paris

very slow: 20 to 23 millions years after the cladogenesis which separated their ancestor, two species of birds or of amphibians are still able to give viable hybrids. On the other hand the genetic evolution of mammals was much more rapid: after 2 or 3 millions years, this aptitude to hybridize is lost.

TABLE I. — Data on interspecific hybridization and generic classification in three groups of vertebrates (after WILSON, MAXSON & SARICH, 1974, PRAGER & WILSON, 1975, and the data of Table II).

Group	Mean age of the divergence between hybridizable species (in millions of years)	Percentage of the "intergeneric" hybridizations among the successful interspecific hybridizations	Mean number of species per genus
Placental mammals	2-3	11	4.04
Birds	20-23	44	4.41
Anuran amphibians	21	3	8.80

If the mean rate of speciation has been similar in these different classes (which is not demonstrated but is not impossible), one expects therefore mammal genera to have a mean number of species lower than amphibian or bird genera. It is indeed what is observed for amphibians, but not for birds. Otherwise, if we consider the rate of "intergeneric", or so called, hybridizations, it is almost null in amphibians, higher in mammals and much higher in birds. These data indicate that supraspecific taxa are probably not equivalent in genetical terms in the various classes of vertebrates. We shall go back again in detail to this problem in the next chapter.

From a morphological point of view, mammalian evolution has been very rapid and diversifying; on the other hand, amphibian evolution has been much slower and less important. Now, the mammals have also lost the ability to hybridize much quicker than the amphibians. According to WILSON and his coworkers, both phenomena would ensue from the same cause: mammals would have undergone more rapid modifications of their systems of genetic regulation. However, the recent results of WYLES, KUNKEL & WILSON (1983) on anatomical evolution in birds indicate that it was as rapid as in mammals, which is not consistent with the just mentioned data concerning hybridization: this indicates that there may exist several types of systems of genetic regulation, which may evolve in a relatively independent way one from another: one would be responsible for the evolution of morphology, and another for the loss of the ability to hybridize. To the best of my knowledge, this latter hypothesis has not yet been proposed or discussed in the literature.

WILSON, SARICH & MAXSON (1974) and WILSON *et al.* (1975) have also underlined the fact that mammals have shown a much higher rate of chromosomal repatterning than amphibians: a rapid evolution of the systems of genetic regulation could therefore be associated with a rapid evolution of karyotypes. The validity of this hypothesis is not demonstrated, and it seems more probable that the evolution of systems of genetic regulation obeys several very distinct modalities, which do not all imply chromosomal repatterning: we shall address this problem again below. However these results point to the interest that the measure of karyological distance between species would have for all works dealing with the evolution and classification of a group. This distance would certainly be correlated with the genetic divergence measured by the synthetic criterion of hybridization.

Source : MNHN, Paris

Hybridization, phenetic similarity and cladistic kinship between species

McAllister & Coad (1978) recently devoted an interesting work to the Cyprinidae of northern America. These authors wanted to compare the classifications of this group such as obtained by the phenetic principles and by the cladist principles. In order to achieve this, they did not compare these classifications directly between themselves, but they compared both of them with a third set of data, those concerning hybridization. Genera were compared two by two. For every one of the 304 pairs of genera on which their analysis bore, the authors calculated a coefficient of phenetic similarity and a coefficient of cladistic kinship between both genera, and they ascertained whether or not natural hybrids between these genera were known. The authors observe that the cladistic classification of this group coincides better with the data of hybridization than does the phenetic classification.

Several aspects of the analysis of these authors are open to criticism. Thus these authors consider that the terms " close taxinomic affinities " on one hand, and " close phylogenetic relationships " on the other, are equivalent: such a postulate is only valid for systematists who adopt the cladist conception of classification; for those who adopt the synthetic conception, both phrases are not synonymous, since genetic and ecological factors must also be taken in consideration, in addition to phylogenetic factors, for the construction of a classification.

Furthermore, McAllister & Coad (1978) consider that the production of hybrids is a measure of close phylogenetic kinship. Now, if it is true that hybridizability expresses an undeniable phylogenetic kinship, this kinship may be more or less recent since, as we have seen, the loss of the ability to hybridize seems to occur at very different speeds from one animal group to another. What the ability to give hybrids clearly expresses, is a great genetic similarity of the two concerned species, this similarity having of course its origin in the fact that these species descend from a common ancestor, but this ancestor being more or less distant.

Other aspects of McAllister & Coad's (1978) analysis may be discussed, in particular the fact that these authors have taken into account only natural hybrids, while, as we have seen, artificial hybrids should also have been considered: in a certain way, these authors have measured by their method the existence of pre-ejaculatory mechanisms of isolation more than the genetic potentiality of the species of both genera to give viable hybrids. Finally their analysis is biased because of the fact that they compared genera, i.e. taxa the nature of which is already determined by the conception of classification chosen (in their case the cladist conception): to avoid any bias of this kind, the analysis should not bear on pairs of genera, but on pairs of species.

Be that as it may, the work of these authors is very interesting from a methodological viewpoint, for it leads to quantify various types of relationships between species and to compare these various measures. Such a work falls completely within the concerns of synthetist systematists, who are neither pheneticist nor cladist, but make use of information of all kinds, phenetic, cladistic, and other, to make a synthesis of them and base their classification on this synthesis.

The different types of " distances " between species

Similarly, and pushing further McAllister & Coad's (1978) method, it could be interesting to make for several distinct and even very different groups of animals overall analyses bearing on different types od " distances " (or "similarities ") between species taken two by two: phenetic distance, " genetic " or molecular distance, cladistic distance, karyological distance, ecological or eco-behavioral distance, and distance measured by the criterion of hybridization.

Source : MNHN, Paris

The comparison of all these data, or at least of the available part of them, would certainly teach us many things, both from the viewpoint of the study of animal evolution and from that of systematics. In many groups the data are still insufficient for such an analysis, but a work of this type could certainly be tackled for the different classes of vertebrates and for several groups of insects.

Several techniques are already available for such an analysis: we shall briefly review them.

Phenetic distance

To the numerous, and now already "classical", methods of numerical taxinomy (SNEATH & SOKAL, 1973), one must now add more recent methods, which are based on a current reflection on the notion of " biological shape " and on the distinction which must be made between the factors " size " and " shape " in the analysis of morphology (JOLICOEUR & MOSIMANN, 1960). Some authors advocate the use of qualitative characters to measure the distance between species or higher taxa (e.g. FINDLEY, 1979), while others, more convincingly, argue that quantitative characters alone allow a non biased analysis (e.g. CHERRY *et al.*, 1979, 1982). Some authors insist upon the fact that the morphology of an organism is the result of its growth, during which, in particular, phenomena of allometry take place, and they try to take these factors into account in the analysis of shape (e.g.: GOULD, 1966; LANDE, 1979; LEMEN & FREEMAN, 1984). On the contrary, others consider that both problems are independent and that the question of the *origin* (in its genetic, ontogenetic and phylogenetic senses) of the morphology of an organism must not be confused with that of the *description* of this morphology and of the *comparison* of the shapes of different species:

> " one must avoid confusing the need for a quantitative description of the degrees of organismal difference with the need for explanations of those differences. " (WILSON, KUNKEL & WYLES, 1984: 1158).

These latter authors have recently studied in detail the problem of the establishment of a reliable index of measurements of morphological or phenetic distance between species taken two by two, in a series of works which are of a great theoretical and practical interest (CHERRY, CASE & WILSON, 1978; CHERRY *et al.*, 1979, 1982; WYLES, KUNKEL & WILSON, 1983; LARSON, PRAGER & WILSON, 1984; WILSON, KUNKEL & WYLES, 1984). Independently from these authors, other biologists have recently addressed this problem of the phenetic distance between species starting from different viewpoints (see e.g.: LAURENT, 1953, 1967, 1981; DUBOIS, 1976).

It is interesting to note that it is only recently that the reflection has really developed on these methods of measurement of phenetic distances. The major reason for that is probably the one emphasized by WILSON, KUNKEL & WYLES (1984) in their answer to a criticism of their previous work (WYLES, KUNKEL & WILSON, 1983) by HAFNER, REMSEN & LANYON (1984):

> " *Two Perspectives in Evolutionary Biology* — It appears to us that the HAFNER *et al.* (1984) criticism is a manifestation of the ' populationist ' perspective, which has dominated systematic and evolutionary biology since the 1940's. It focuses on the *tips* of the evolutionary tree and on the uniqueness of every trait, individual, population and species (...). In contrast, we have been influenced by what might be termed the ' distance ' perspective, which entered evolutionary biology more than 20 years ago as biochemists began to compare proteins from species belonging to different *branches* of the tree (...).
>
> The ' populationist ' perspective's emphasis on uniqueness engenders respect for the generalisation referred to by HAFNER *et al.* (1984): The set of characters that best discriminates among members of one taxinomic group is unique to that group. Such perspective makes one wary of comparing the degree of difference between a pair of species in one taxonomic group with that in another taxinomic group. Molecular evolutionists, by contrast, have long been comfortable with the pratice of using the same yardstick (i.e., number of substitutions) to examine and compare evolution in vastly different taxonomic groups. The criticism of our work by HAFNER *et al.*

Source : MNHN, Paris

(1984) has made us realize what a deep gulf there is between these two perspectives and how important it is to explore that gulf on another occasion." (WILSON, KUNKEL & WYLES, 1984: 1158-1159).

This problem meets that of the "gap" which exists between the "populational" approach to the study of evolution and the study of macro-evolutionary phenomena: we shall come back to this problem in more detail below.

"Genetic" distance

This expression classically designates distances like NEI's (1972) or ROGERS's (1972), which are based on the results of protein electrophoreses. This distance is very badly named, since it only measures in the fact the divergence at the level of a few structural genes, without taking at all into account the divergence at the level of systems of genetic regulation, and a phrase like "molecular distance" would certainly suit it much better. PASTEUR (1985) recently gave a discussion of the different types of "genetic" distances based on the results of protein electrophoreses which are currently in use. Other types of "genetic" distances must be added to these, like "immunological distance" based on the micro-complement fixation method (WILSON, CARLSON & WHITE, 1977; PASTEUR & PASTEUR, 1980), or the distances based on DNA hybridization (SIBLEY & AHLQUIST, 1982; DIAMOND, 1983).

Cladistic distance

To measure such a distance, one could make use of the coefficient proposed by MCALLISTER & COAD (1978).

Karyological distance

Some authors, like WILSON, SARICH & MAXSON (1974) or COTHRAN & SMITH (1983), calculated a karyological or chromosomal distance on the basis of the number of chromosomes and the number of chromosomes arms of the compared species. In the future, it would be necessary to have a more precise, finer measurement of karyological distance, for the same chromosome number and the same fundamental number may be obtained in a totally independent manner in different species. A finer comparison could for example take into account the total quantity of nuclear DNA as well as the place of constrictions and of bands revealed by the techniques of banding (DUBOIS, 1983 a: 56-57). This will only be possible in the case of groups which have already been the subject of a rather advanced cytogenetical study. Thus MARTIN & HAYMAN (1965) proposed to compare karyotypes of closely related species, a method which takes into account the relative lengths of the arms of chromosomes and the relative quantities of DNA by genome; as far as they are concerned, PREVOSTI, OCAÑA & ALONSO (1975) proposed an index based on the differences of frequencies of chromosomal arrangements to measure a distance between populations of the genus *Drosophila*.

Ecological or eco-behavioural distance

Works where ecological or eco-behavioural distances between species have been estimated are still rare, although such distances would be very interesting. At the moment the interspecific distances which have been measured in this field concern only certain aspects of the ecology and behaviour of the species: e.g. distribution of the species in microhabitats (ORTEGA, MAURY & BARBAULT, 1982), techniques and sites of alimentation (LANDRES & MACMAHON, 1980), trophic spectra of the species (BARBAULT, 1981: 119), characteristics of the mating calls of males (DUELLMAN & PYLES, 1983). In his interesting 1978 work on an equatorial community of amphibians and reptiles, DUELLMAN calculated somewhat more complex distances, which take into account various types of parameters (habitat, vertical distribution, periods and types of activities, feeding, size, mode of reproduction, characteristics of males mating calls). It would certainly be interesting to develop research in this direction, and to construct overall indexes of eco-behavioural similarity between species, which could take into account the physico-chemical characteristics of the niche occupied by every

Source : MNHN, Paris

species (climatic and microclimatic parameters, pedological parameters, etc.), as well as certain biological parameters allowing a characterization of this niche in demographic terms, in terms of biomass and of energy flux, and of parameters drawn from behaviour (e.g. bio-acoustic characteristics of sound emissions, etc.). It would certainly be most instructive to compare such distances with the other distances mentioned here. For example, it is not unreasonable to think that the overall morphology of a species (its " shape ") expresses in a certain synthetic way the ecological niche of this species, and it is likely that the divergence between two species in one or another of these fields is correlated with their divergence in the other. It is to be wished that ecologists got interested in these problems and proposed methods allowing such estimates. In the meanwhile, one must recognize that the notions of ecological niche and of adaptive zone, although fundamental in the interpretation of evolutionary phenomena in the light of the synthetic theory, still remain very little functional. This is in my opinion the field in which the most important progress remains to be made for a truly synthetic appraisal of evolutionary facts.

Hybrid distance

What has been said above shows that it would be very interesting to have a distance index between species measured by the criterion of hybridization. For more simplicity, I propose to designate such a measurement by the name of " hybrid distance ". As was already emphasized (DUBOIS, 1983 a: 58), the following stages of development of hybrids seem to be generally valid for the whole animal kingdom, and could constitute the framework for a unique scale of measurement of this distance:

(1) failure at fertilization;

(2) failure at the beginning of the gastrula stage;

(3) failure during the postgastrulean embryonal, larval, or young stages;

(4) infertile adult animals, or adult animals having a disturbed progeny;

(5) fertile adult animals with a normal progeny.

To this rough scale, it should soon be possible to add a finer scale for the crosses which lead to the development of a hybrid, at least in the first stages (levels (3) to (5) in the scale above). In this respect, the way was opened by PARKER, PHILIPP & WHITT (1985 a, 1985 b), who proposed to use various indexes to estimate what they call the " regulatory distance " between two species able to hybridize: percentages of fertilization and or hatching of hybrid eggs, extent of the disruptions in the temporal expression of various enzymes during embryonic development (in relation to the normal temporal expression in one of the two species crossed), extent of the disruptions in the rates of activity of these various enzymes (in relation to the normal rates of activity in one of the two species crossed). At the moment these are only several distinct indexes which give sometimes somewhat different results, but it is not forbidden to think that it will be possible in the future to combine these various data into a single " hybrid distance " index between two given species. To be able to do this, however, it will be necessary to study the relationships which exist between the different criteria mentioned here: some of them give similar results, others very divergent ones. It is probable that these criteria are not independent one from another, and it is therefore not possible, at the moment, to calculate a single overall index of " hybrid distance " simply by adding the values of the different indexes (WHITT, 1985). Given the variability of results, at all levels, of hybrid crosses (according to the direction of the cross, to the populations and individuals used, etc.), it is at any rate probable that such an index should not be based on a *mean* of the results observed, but rather on the *best results* obtained, as we have seen above.

It is clear, as emphasized by PARKER, PHILIPP & WHITT (1985 a, 1985 b), that the relative success of development of the various types of hybrids expresses in a synthetic way the importance of the divergence which has occurred between the two compared species at the level of their systems of genetic regulation. It would therefore be most interesting in the future, as well from the viewpoint of the study of evolutionary mechanisms as from that of supraspecific systematics, to develop methods of measurement of " hybrid distance " between species.

Source : MNHN, Paris

Source : MNHN, Paris

INTERSPECIFIC HYBRIDIZATION AND THE CONCEPT OF GENUS IN ZOOLOGY

HYBRIDIZABILITY AS A CRITERION FOR THE DEFINITION OF GENERA

BRIEF HISTORICAL SURVEY

The criterion of hybridizability has until now been only very little used by systematists to recognize taxa above the species level. It is true that as early as in the 19th. century some authors had tried to do it (see in this respect FISCHER, 1981). Thus FLOURENS (1856: 6) wrote:

> " The *species* is characterized by the *continuous* fertility; the *genus* by the *limited* fertility " (translation mine),

and he considered that two species like the donkey and the horse or like the jackal and the dog, able to produce hybrids between them, should be placed in the same genus (see also FLOURENS, 1845 a: 298-301; 1845 b: 119-128).

More recently, GHIGI (1936) proposed to use the hybridization criterion in macrotaxinomy: he suggested that according to the degree of success of the hybridization between two species (success measured by the degree of fertility of the F1 hybrids of both sexes), these species be referred to the same genus, to different genera or to different families. In the same spirit, KINSEY (1936, in SIMPSON, 1937: 265) writes:

> " The capacity of two groups to hybridize is inversely correlated with their categorical rank. "

Similar ideas were more recently expressed by HUBBS & DREWRY (1960). Other authors have mentioned in passing the theoretical possibility of admitting that species liable to give viable hybrids between them should be placed in the same genus (see e.g.: SIMPSON, 1961: 90, note 10; SHORT, 1969: 87; HUBBS, 1970; PÉPIN *et al.*, 1970), but these proposals had no claim to a general value. In the recent years, finally, three different authors (VAN GELDER, 1977, 1978; PLATEAUX, 1981; DUBOIS, 1981 a, 1981 c, 1982 a, 1983 a) independently made a similar proposal, giving it a general value for the whole animal classification and justifying it by rather different, albeit not contradictory, arguments. This convergence is interesting: it shows in my opinion that times are ripe for the use of such a criterion in zoology.

The main argument presented by VAN GELDER (1977) to justify this proposal is the need of a certain internal coherence of the classificatory system between the notion of species, defined by a mixiological criterion, and that of genus:

Source : MNHN, Paris

> " Basically, the logic of a reproductively isolated and self-contained genus seems inescapable if one accepts the *concept* of the reproductively isolated species. The genus neither can nor should be of less dimension than the species, and if the parameters of the species are ultimately established by its reproductive capabilities, then the genus, too, must be so proscribed. The greatest extent of reproductive compatibility allowed between species is generally the production of sterile offspring. The production of fertile offspring in nature is usually sufficient grounds for merging the parental stocks into a single species with their recognition only as subspecies. Similarly, for allopatric species, captive hybridization with fertile offspring may be used to consider the parental stocks conspecific. If these are the reproductive limits of species it would seem to follow that the genus must be reproductively at least, if not more, separable, and that crosses between genera be wholly incapable of producing a live offspring. " (VAN GELDER, 1977: 18).
>
> " (...) the upper limit for the species (reproductive incompatibility) should also be contained in the definition of the genus, and at least represent its lower limit. This would imply that intergeneric hybrids should not be possible by so defining the genus. The arbitrariness of the definition of the genus exists in its width and upper reaches, not at its interface with the species, where its definition is the same as that of a species. " (VAN GELDER, 1977: 4).

As far as he is concerned, PLATEAUX (1981) justifies his proposal mainly by an argument of " common sense ". Using the term " syngameon " (in the sense of CUÉNOT & TÉTRY, 1951) to designate a group of species liable to hybridize, he writes:

> " If the syngameon can come to include several genera, the genus does not mean much any more. One could think of replacing it by the syngameon, but the latter is usually not yet delimited. It is better to consider something wider. But, at least, it should be a group the lower limits of which may be traced before they join those of the species!
>
> It seems to me that one could take the strict rule not to place in different genera species able to produce together fertile hybrids, even if this fertility is only very partial. In most cases, it would even be wiser to place in a same genus all the species able to produce between them hybrids of any kind. " (PLATEAUX, 1981: 518; translation mine).

As far as I am concerned, I made very precise propositions for the use of a criterion of hybridizability in animal systematics, on the basis of the preceding analysis (DUBOIS, 1981 a, 1981 c, 1982 a, 1983 a, 1985 b). Let us now examine these propositions in detail.

PRECISE FORMULATION OF THE CRITERION AND OF ITS CONDITIONS OF USE

The first point to insist upon here is the fact that the success or the failure of hybridization does not at all have the same meaning or importance. A single gene brought by one of the parents may be enough to prevent the development of a hybrid zygote, even though all other genes are compatible (example of the *Lhr* gene of *Drosophila simulans*, discussed above). The failure of hybridization indicates that the two populations of which the individuals are intersterile do not belong to the same species. It does not tell us anything more about the genetic and phylogenetic relationships between both species. The same is true for the infertility of some adult hybrids: it can be due to several types of causes, some of which involve only a few genes or even a single gene, and it is therefore of rather unclear meaning. The factors of lethality and of infertil-

Source : MNHN, Paris

ity of hybrids being very diverse, it is impossible to take into account the negative results of hybridization (lethality during development, infertility of adults or failure in F2) for a phylogenetic and genetic analysis of the relationships between species. For not having realized that, some authors have believed that hybridization could be of no use in supraspecific systematics, while only its negative results would be.

On the other hand, positive results give very interesting information: if it is rather easy to prevent the development of a zygote issued from two very closely related species, it is impossible to do the contrary, i.e. to obtain a normal development starting from a diploid egg issued from the hybridization of two distant species. Given the complexity of the genome of eucaryotes, it is quite out of the question that two genomes could be functionally compatible by convergence or by chance. The compatibility of two genomes proves that the two species which bear them descend from a relatively recent common ancestor, from which they have conserved the homologous parts of their genomes. The criterion of hybridizability has therefore both a genetic and a phylogenetic meaning, although its phylogenetic meaning is less clear and more ambiguous than its genetic meaning, since the loss of the ability to hybridize occurs at a different speed in various animal groups.

My proposition is therefore to consider that when two species are liable to give rise between them to viable adult hybrids, these two species must be included in a same genus. Let us remember that these are true diploid hybrids, possibly obtained in experimental conditions, which may be fertile or not, and finally that we only take into account the best result observed in various crosses between two species, possibly in some only of the types of crosses which may be realized between them (e.g. male of one species with female of the other, but not the reverse, or animals coming from certain populations only).

The criterion of hybridizability must therefore be used only in one direction, to *group together* species in a same genus, but not to separate genera: when viable adult hybrids may be obtained between the species A and B, these species belong to the same genus; on the other hand if hybridization does not occur or if the hybrids are not viable, no information is given and the criterion must never be used to place two species in two distinct genera.

We have here, according to SIMPSON's (1951, 1961) terminology, a *nonarbitrary criterion as to inclusion*, but which must never be used for exclusion:

> " A group is nonarbitrary as to inclusion if all its members are continuous by an appropriate criterion, and nonarbitrary as to exclusion if it is discontinuous from any other group by the same criterion. It is arbitrary as to inclusion if it has internal discontinuities and as to exclusion if it has an external continuity. " (SIMPSON, 1961: 115).

A second very important point is the fact that this criterion takes into account the *genetic potentialities* which exist to build an organism, and not at all the fact that hybrids do exist or not in nature, various " parasitic " factors (in particular eco-behavioural and geographical ones) being liable to be responsible for their absence. The criterion is obviously all the more valid when natural hybrids do exist, but the use of the criterion to *group together* species in one genus only implies the ability to obtain adult hybrids between both species, even if for this it has been necessary to call upon particular techniques, like artificial insemination and fertilization, or even more elaborate techniques aiming at solving certain specific problems (e.g., in amphibians, " ROSTAND's technique ", described above).

Obviously, this criterion is not used alone: it intervenes as a new and additional piece of information but it does not nullify all the other pieces of information which had already been gathered, by the other more " classical " methods, on the species considered. Thus, before the hybridization between species A and B was observed, these two species may have been placed in two distinct genera I and II, on the basis of other criteria (morphological, molecular and ecological resemblance, data on the phylogeny of the group, etc.). The fact that these species prove able to give adult hybrids must first

Source : MNHN, Paris

prompt the systematist to a critical reappraisal of the validity of taxa I and II: it might well be that these taxa, or one of them, constitute artificial groupings, e.g. placing together species of different phylogenetic origins and resembling each other by convergence, or that one of both species A and B has been placed by mistake in the genus I or II but belongs indeed to the other one. The results of hybridization may thus suggest the realization of works of systematic revision at the generic or familial level and lead to rectify certain mistakes. However it frequently happens that the revisional work leads to a confirmation of the validity of groups I and II and the respective membership in these two groups of the species A and B. The fact that these two species are hybridizable implies then not only that they should be grouped together in a same genus, but also that all the other species which by other criteria were classed in the same genus as A and in the same genus as B be placed in this genus — in other words to group the former genera I and II together in a single genus. If both groups are separated by a certain morphological, ecological, or other, discontinuity, it may be well to retain for them the status of distinct subgenera within the new genus. It is important to emphasize that the fact that a single pair of species belonging to the former genera I and II gives adult hybrids is enough to group both genera together, even if no other pair of species of the two genera is known to give viable hybrids. As a matter of fact to require that all species of both genera be hybridizable two by two and to refuse to join the genera if they are not would come down to use the negative results of hybridization for the construction of the classification, and we have seen on the contrary that only positive results may be used for this aim.

To sum up, the new criterion may be formulated as follows: *when two species are able to give birth to viable adult hybrids, be these fertile or not, both species must be included in the same genus; furthermore, if these two species had previously been attributed, on the basis of valid criteria, to two distinct genera, the latter should be merged together.*

Taxinomic characters and relational taxinomic criteria

The word "classification" is used in two distinct senses (Mayr, 1969: 4): (1) to designate the product of the activity of taxinomists; (2) to designate classificatory activity itself. Mayr (1982 a: 185) proposed the following definition of classification as an activity:

> "Classification is the ordering of organisms into taxa on the basis of their similarity and relationship as determined by or inferred from their taxonomic characters."

As for the notion of taxinomic character, Mayr (1969: 121) defines it as follows:

> "A taxonomic character is any attribute of a member of a taxon by which it differs or may differ from a member of a different taxon."

These definitions are those of a synthetist systematist. As far as they are concerned, cladists, who have devoted an important reflection to the concept of character and to the analysis of characters (Dupuis, 1979, 1984), proposed slightly different definitions. For example Wiley's (1981: 116) definition reads as follows:

> "A *character* is a feature of an organism which is the product of an ontogenetic or cytogenetic sequence of previously existing features, or a

Source : MNHN, Paris

feature of a previously existing parental organism(s). Such features arise in evolution by modification of a previously existing ontogenetic or cytogenetic or molecular sequence."

According to these definitions, or to equivalent definitions which could be found in many other works, (1) classification is based on taxinomic characters, and (2) taxinomic characters are attributes of the organisms that one wants to classify.

The construction of a classification requires therefore a two-step procedure: (1) *analysis* of taxinomic characters of the to-be-classified organisms; (2) *comparison* of these organisms on the basis of the results of this analysis.

This process is summarized for example by SIBLEY (1965: 114), who writes:

> "There is, in systematics, only one basic technique, that of *comparison*. Because comparisons between whole organisms present insuperable difficulties it is customary, in fact necessary, to compare *characters*."

From this viewpoint, there exists no difference between the various conceptions of systematics currently in existence: they all construct classifications on the basis of characters, which are recorded on individuals; on the other hand what distinguishes these conceptions are the methods of comparison used, some of which (cladists, synthetists) rely on an analysis of the evolution of characters in a lineage (plesiomorphous to apomorphous characters), while others (empirists, pheneticists) do not.

The importance of the analysis of characters (be these morphological, molecular, ecological, etc.) in systematics is considerable, and it is not my intention to negate it. However I think that it is not only on this basis that classifications can be built. This fact is particularly obvious at the level of the key-category of Linnaean taxinomy, that of species, as I have already emphasized:

> "There exist no 'morphological' species, no 'ecological', 'genetical', etc., species, not even 'biological' species: all species of living beings are 'biological'! There does not exist either 'criteria' for the species, or, rather, there exists only one, which is the coincidence between natural reality and the 'theoretical' concept of species. Several 'criteria' do exist which allow one to differentiate individuals (or groups of individuals) within populations, or populations, and to quantitatively appreciate the importance of divergences, but none of these criteria by itself tells us if the observed differences are of a specific 'nature'. The importance of divergences between populations will be liable in certain cases to give us clues for example on the duration of the separation which may have existed between them, but it will not allow us to know if these remain able or not, e.g. on the occasion of a new geographical contact between them, to merge together and constitute again a single genic pool. Except for the karyological and mixiological criteria, and, even there, (...), in certain cases only, no criterion allows one to assert that the step of speciation has been crossed between two populations or groups of populations." (DUBOIS, 1977 b: 205, translated).

As a matter of fact, the only true "criterion" of the species is the conformity with the definition of "protected gene pool", whatever the method used to demonstrate it. It is true that generally the decisions of systematists at this level are dictated by the analysis of characters, but they may sometimes derive from the use of other criteria, such as that of the existence or non-existence of a natural hybridization between two sympatric or parapatric groups of animals. This existence or non-existence may sometimes itself be demonstrated by the analysis of characters, but sometimes by other methods, like the observation of the behaviour of the animals of both groups when they are in contact. The criterion then used bears on the *type of relation* which exists between both groups of organisms compared. It is a *relational taxinomic criterion*,

Source : MNHN, Paris

which is interested in the particularities of the relation between these organisms, but not in the attributes of these organisms taken one by one.

The criterion of hybridizability, which I propose to use in supraspecific systematics, is precisely a criterion of this type. Its use demands the study of the interaction which takes place, not in nature between two groups of individuals, but, this time, between two species when their genomes must collaborate to build an organism together. In a sense, it is the species themselves which compare themselves, not an outside observer. In this sense, the criterion of hybridizability is an objective, nonarbitrary criterion, which makes the genus a " natural " taxon, in the same sense as the species.

Classification can therefore not rely upon the single analysis of characters. It demands a synthetic approach, and the use, in addition to the taxinomic characters (proper to any of the compared organisms taken separately), of relational taxinomic criteria which are based on the properties of the relation which exists, in nature or in experimental conditions, between the organisms compared.

For this reason, I think that MAYR's (1982 a) definition of classification given above cannot be retained. I advocate rather the use of a definition which is not based on the concept of taxinomic character, like for example those proposed earlier by MAYR (1969):

> " *Classification.* The delimitation, ordering, and ranking of taxa. " (MAYR, 1969: 400).
>
> " *Biological classification.* The arranging of organisms into taxa on the basis of inferences concerning their genetic relationship. " (MAYR, 1969: 399).
>
> " Zoological classification is the ordering of animals into groups on the basis of their similarity and relationship. " (MAYR, 1969: 55).

In what precedes, I mentioned two relational taxinomic criteria, one of which is useful at the level of the species, and the other one at the level of the genus. Both criteria are based on facts of hybridization, and one could think that it is only around these facts that such criteria could be proposed. This is not true, just as it would not be correct to consider that both criteria mentioned above are of the same type. As a matter of fact the relational criterion used at the level of the species (existence or not of hybrids in nature and of a genic flux between both groups of sympatric or parapatric animals) is highly synthetic, since it takes into account both eco-behavioural or morphological phenomena (existence or not of pre-ejaculatory mechanisms of isolation between species), and genetic and developmental phenomena (existence or not of post-ejaculatory mechanisms of isolation). On the other hand, the criterion of hybridizability used at the level of the genus takes only into account genetic and developmental phenomena, since it is only interested in the existence or not of postzygotic mechanisms of isolation between species.

Conversely, one can perfectly imagine, although at the moment their use is virtually non existent in systematics, relational taxinomic criteria which would take into account other phenomena than genetic or developmental ones, e.g. ecological phenomena. A good example in this field is that of the criterion proposed by ILLIES (1970) to define genera — a criterion which, to my knowledge, has been received with complete indifference by zoologists until now. Basing himself on MONARD's (or GAUSE's) principle, according to which two species having very similar or identical ecological niches cannot live in sympatry, this author proposed to consider the ecological coexistence of two species as a criterion of membership of the latter in two distinct genera. Whatever may be thought of the validity of this criterion (see below), it is undeniably a relational taxinomic criterion.

The use of such criteria is justified in a " synthetic " perspective of zoological classification, but would have little meaning for systematists adopting the empirical, phenetic or cladist conceptions of classification. These criteria are in fact totally incompatible with any *typological* conception of classification (MAYR, 1969, 1982 a). They allow one to put once and for all an end to the notion of " *typical* " *character*, to the conceptions according to which an organism would have two kinds of characters, some " specific ", some " generic ", " familial ", etc. One must class *organisms*, not characters, which was already expressed by LINNAEUS (1751: 119) when he wrote:

Source : MNHN, Paris

" *Characterem non constituere Genus, sed Genus Characterem. Characterem fluere e Genere, non Genus e Charactere. Characterem non esse, ut Genus fiat, sed ut Genus noscatur* ".

In a synthetic conception of classification then, the genus could not " rest " on a single character, on a presence/absence dichotomy in a determination key. On the contrary genera can be *polythetic* (SNEATH, 1962; MAYR, 1969; SNEATH & SOKAL, 1973), i.e it can well be that certain species do not possess some particularities "characteristic " of the genus, that no " diagnostic " character be common to all species of the genus. This is contradictory to an attitude still rather frequent among some systematists, and which is well expressed for example by ALPHÉRAKY (1912: 36, translation mine):

> " Every Species, or member of a Genus, must absolutely possess *all the characters* proper to the Genus, and if one of them possesses, be it only one single additional character, or if it lacks one, it must be excluded from this Genus and placed in a distinct Genus ".

Needless to say, from a purely empirical and pragmatical viewpoint, the opinion expressed in this citation is perfectly justified. It is not so insofar as one considers that systematists must try to recognize only taxa which correspond to natural evolutionary units, and not "pigeonholes " aiming at facilitating the identification of specimens.

THE CRITERION OF HYBRIDIZABILITY AND THE PROBLEM OF THE EQUIVALENCE OF HIGHER TAXA

INTRODUCTION

One of the main interests of the new criterion of hybridizability is that it permits a standardization of systematics in the whole animal kingdom, and that it allows one to solve in part the problem, which has preoccupied many systematists (e.g.: HENNIG, 1950, 1966; CROWSON, 1970; VAN VALEN, 1973; SCHAEFER, 1976; SIBLEY & AHLQUIST, 1982), of the equivalence of higher taxa in different groups. By making use of this criterion, in a certain way a genus of ants would be equivalent to a genus of mammals. It would of course be so only partly, in particular because the criterion is not symmetrical and cannot always be used, problems which we shall discuss again below, but it would nevertheless make for important progress in this direction.

The comparative study of classifications is the field of " comparative systematics ", in the sense of MAYR & SHORT (1970) and of BOCK & FARRAND (1980). As was emphasized by the latter authors, this domain is still little explored:

> " Comparative systematics is a new area of inquiry within taxonomy, so recent that it has not been discussed in general texts on systematics and its major goals have not yet been clearly formulated. A preliminary statement of the goals of comparative systematics may be — the analysis of the structure and composition of taxa (i.e., the number of component subgroups in each taxon and their nature) and of their evolutionary history. These goals may change as more is learned about the comparative systematics of diverse groups of organisms. " (BOCK & FARRAND, 1980: 22).

Source : MNHN, Paris

However, the need to have criteria of standardization and of comparison, permitting the recognition of equivalent taxa in different groups, is not due to a whim or simply to a taste for " intellectual elegance ". As was emphasized in particular by MAYR (1969, 1974, 1981, 1982 a), zoological classification must not only be an identification system, but also a true theory, in the light of which all biological facts find their true meaning.

The works of the last years on various aspects of biological evolution fully confirm this viewpoint. More and more frequently indeed, classification is taken as a system of reference to interpret the results of comparative works carried out in the most varied fields (molecules, morphology, behavior, ecology, etc.). Let me give a few examples. It is on the basis of the current classifications of these groups that PRAGER & WILSON (1975), CHERRY, CASE & WILSON (1978), CHERRY *et al* (1982) and WYLES, KUNKEL & WILSON (1983) have pointed to the disparities of the rates of morphological, karyological and molecular evolution in the different classes of vertebrates. Similarly, it is on the basis of these classifications that AVISE & AQUADRO (1982), AQUADRO & AVISE (1982) and others have estimated that evolution at the level of structural genes has been slower in birds than in other vertebrates, results which are disputed by SIBLEY & AHLQUIST (1982). Finally, it is on the basis of the current classification of teleosts that WHITT, CHILDERS & CHO (1973), CHAMPION & WHITT (1976), PHILIPP, CHILDERS & WHITT (1979), PHILIPP, PARKER & WHITT (1983) and PARKER, PHILIPP & WHITT (1985 a, 1985 b) have asserted that the disruption of allelic expression in certain hybrids (inhibition of certain alleles, modification of the rates of expression of certain other ones, etc.) is a function of the " systematic distance " between the hybridized species. Such " systematic distances " are more and more used, and compared with the other types of distances (" genetic ", phenetic, karyological ones, etc.) discussed above. It is evident that such a practice is meaningful only if classification is based, at least in part, on objective, nonarbitrary criteria, and is not completely empirical. It becomes thus more and more urgent, as synthetic works of this type multiply, to find criteria having a general value for all animal groups.

One could believe that the only category allowing such a hope is that of the species, since it is only at this level that genetic material is exchanged and that real genetic units do exist in nature, independently from the interpretation which we can make of it. Once speciation has taken place, there does not usually (with a few exceptions) exist genetic exchanges between the individuals of two different taxa, and it would be necessary to abandon the hope of recognizing " natural " or " equivalent " groups. However we have seen above that, at the level of the genus at least, it is possible, by taking into account the results of artificial hybridization (then not only phenomena which occur spontaneously in nature), to recognize " natural " units, on the basis of a criterion which relies only upon the properties of the cross realized between two species. This criterion allows one to recognize taxa which are equivalent from one group to another. It is not the only one in this case, and we shall now devote a deeper study to the various criteria of this type.

THE CRITERIA OF EQUIVALENCE BETWEEN TAXA

SCHAEFER (1976) has addressed this problem of the equivalence of taxa in different groups. He considers it insolvable, because of the absence of common criteria between different groups:

> " In short, it seems not likely that higher categories can be made equivalent even in related groups. I do not think the reasons are obscure. For there to be bases for establishing equivalence, there need to be some common criteria: either common adaptations to the same or different environments, or perhaps different adaptations to the same environment. Family-groups with the same adaptations to the same environment are *ipso facto* not different family-groups, if by ' same adaptations ' we mean

Source : MNHN, Paris

genetically the same. It is improbable that two groups would arrive at or achieve, the same adaptations to different environments, since the environment after all culls from the genetic variety, and different environments will not cull the same adaptations from that variety.

The possibility of different adaptations to the same environment is more interesting. Fish and cetaceans are adapted to roughly the same environment, as are kangaroos, bison and African antelope: Can the family-groups here be made equivalent? I much doubt it. Equivalence is a taxonomic judgment, and such judgments are based on assessments of genetic similarity. Where there is no genetic similarity, such judgments as equivalence cannot be made. However similar the adaptations of different groups to the same environment may appear, these adaptations will not bear close scrutiny; they are only superficially similar, having been attained by different genetic routes; they therefore cannot be compared except superficially." (SCHAEFER, 1976: 2).

As far as he is concerned, VAN VALEN (1973) tried and built a list of the criteria which could be used to compare taxa from one group to another, and which prove more numerous than those considered by SCHAEFER (1976). The following list is inspired by that of VAN VALEN (1973), to which however appreciable modifications have been brought.

Phenetic criteria

A first criterion could be phenotypic diversity (VAN VALEN, 1973: 334). This could be estimated on the basis of the phenetic distances discussed above. Such a measure would be interesting for *comparing* taxa (and possibly to deduct from this certain modalities of their evolution), but, as remarked for example by LEMEN & FREEMAN (1984: 1236), they would not at all allow the *definition* of supraspecific taxa, just like species cannot be defined by their intraspecific variability.

"Genetic" or molecular criteria

A second type of criterion contemplated by VAN VALEN (1973: 334) is that of genotypic (or genetic) diversity. As was shown by all the preceding discussion, such a measurement poses many problems. In VAN VALEN's (1973) mind, such a diversity could be estimated by the diversity of proteins (indirect method) or of DNA (direct method). In reality, as we have seen, an index of this type would inform us about the structural divergence between the genomes compared, but not about their functional differences. However, because the evolution of structural genes is largely proportional to time, an index ot this type could possibly allow one to estimate the age of taxa. We will come back to this aspect below.

Ecological criteria

VAN VALEN (1973: 333-334) considers the possibility of using an ecological criterion to compare taxa from one group to another only in a relatively restricted way: he proposes to estimate the number of individuals, or the biomass, or the energetic value, represented at a given moment by the group. In a certain way, such a measure would give an idea of the "evolutionary success" of a group. However the groups which have the highest number of individuals are probably not the same as those which have the highest biomass or energetic value. Furthermore, the "ecological success" of a group may not necessarily be measured in quantitative terms: some species produce relatively few descendants at each generation, but these have a high survival rate, while others produce a large number of descendants but which undergo a high mortality at each generation. Eventually, the only real measure of the "success" of a group is its survival and perpetuation, and only the relative *extinction* of species in different groups could give us a negative estimate of it (see also on this question WAKE, ROTH & WAKE, 1983).

Other ecological criteria could be used, for example ecological diversity, estimated on the basis of the "ecological distances" mentioned above. Independently from the practical problems raised by such a mesure, it would raise the

Source : MNHN, Paris

same theoretical problem as the phenetic distance discussed above: it would allow the comparison of taxa, but not their definition.

ILLIES (1970) recently proposed an interesting criterion to define genera: the ecological coexistence of two species would be considered as meaning that these must be referred to two distinct genera. This is a nonarbitrary criterion as to exclusion, in the sense of SIMPSON (1951, 1961). As we have seen, this is a relational taxinomic criterion, like that of hybridizability. However, despite its interest, this criterion does not seem to be utilizable for recognizing genera. As a matter of fact, if it is true that the ecological niches of two species cannot be identical, there often exists a wide overlap between the niches of the species which occupy a same adaptive zone, the latter being wider than any of the niches which compose it. The application of the ecological exclusion criterion proposed by ILLIES (1970) would lead in practice to multiplying the names of genera considerably, and to empty the notion of genus of almost all phylogenetic meaning. It could however be interesting to explore this type of criterion in more detail, by taking into account not only the spatial dimension of the niches of species (coexistence) but also other dimensions of the latter (competition at the level of resources, of the acoustic niche, etc.). Criteria based on such analyses could prove useful to define certain supraspecific and infrageneric taxa (subgenus, species group, etc.).

Absolute age of taxa

An attractive criterion to make taxa equivalent from one group to another is that of the absolute age of taxa. This criterion, first proposed by HENNIG (1936, 1950, 1966) and adopted by several authors (KIRIAKOFF, 1954, 1965; CROWSON, 1970; etc.), raises practical problems of application which appeared insuperable a short time ago (see e.g. the discussion of this question in DUPUIS, 1979: 47-50). Recently, SIBLEY & AHLQUIST (1982) asserted that the methods of hybridization of the DNA would allow one to reliably date the cladogeneses which have separated lineages leading to contemporaneous species, and suggested the use of this criterion to ascertain the ranks of taxa. Actually, as was emphasized e.g. by SIMPSON (1962) or MAYR (1969: 72, 230; 1974), and as was recalled above, the use of such a criterion has a meaning only within the frame of the cladist conception of classification (the latter being supposed to be a direct translation of the phylogenetic tree), but not within that of the synthetic or evolutionary conception of classification: the attribution of the same rank to taxa of the same age, independently from the

TABLE II. — Number of living taxa in the four major categories of the Linnaean taxinomic hierarchy (species, genus, family, order) in the six classes of Vertebrata Gnathostomata, and positions of these categories in the distance species-class, calculated according to VAN VALEN's (1973) method of analysis, slightly modified: here the categories species and class have been chosen for the extremities of the axis (with the respective values 0 and 1), and the position P of any other category is given by the relation $P = (1 - R) \times 100$, where R is the ratio of the logarithm of the number of taxa of this category to the logarithm of the number of species in the class (this position may also be determined graphically, as shown by VAN VALEN, 1973).

N = number of taxa of the category in the class.
P = position of the category.
Sources for the numerical data on taxa: (1) NELSON, 1984; (2) DUBOIS, 1985 a; (3) FROST, 1985; (4) DUELLMAN, 1979; (5) BOCK & FARRAND, 1980; (6) ANDERSON & JONES, 1967; (7) VAN GELDER, 1977, 1978.

Class	References	Species (S) N	Genera (G) N	Genera (G) P	Families (F) N	Families (F) P	Orders (O) N	Orders (O) P
Chondrichthyes (CH)	1	793	151	24.8	25	51.8	6	73.2
Osteichthyes (OS)	1	20857	3881	16.9	418	39.3	42	62.4
Amphibia (AM)	2,3	4015	395	27.9	36	56.8	3	86.8
Reptilia (RE)	4	5954	885	21.9	46	55.9	6	79.4
Aves (AV)	5	9021	2045	16.3	160	44.3	28	63.4
Mammalia (MA)	6	4060	1004	16.8	122	42.2	20	64.0
"	7	—	960	17.4	—	—	—	—

Source : MNHN, Paris

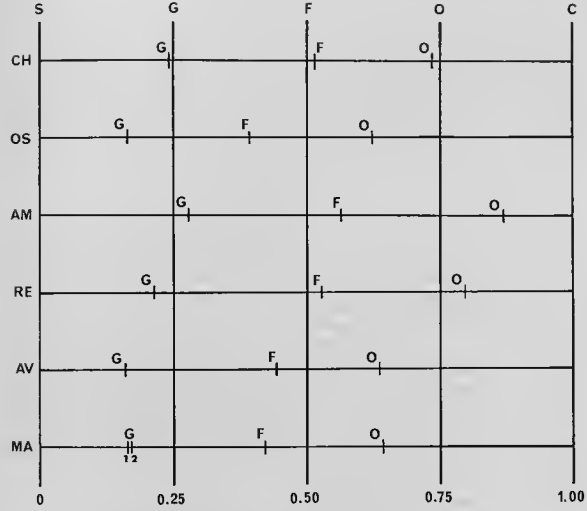

FIG. 2. — Positions of the major categories of the Linnaean taxinomic hierarchy in the six classes of gnathostome vertebrates (living species only, from the values of Table II).

In a strictly " balanced " or " symmetric " classification, the positions of the intermediate categories would be regularly spaced between the two extremities (0.25 for genus, 0.50 for family, 0.75 for order). When the observed values are lower than these " expected " values (i.e. when the observed point is to the left of the vertical line corresponding to the " expected " value), the classification of the class may be described as " oversplit " according to VAN VALEN's metataxinomic criterion; on the contrary, when these values are higher than the " expected " ones (or the point to the right of the vertical line), the classification may be described as " overlumped " with respect to this criterion.

For the meaning of the abbreviations, see Table II. For the class of mammals, the position of the category genus is shown according to two different generic classifications (see text): (1) ANDERSON & JONES, 1967; (2) VAN GELDER, 1977, 1978.

Source : MNHN, Paris

fact that they may or may not have experienced an important divergence or diversification since their appearance, greatly reduces the information contents of the classification, which does not give any more indications on the different evolutionary rates from one group to another, on the shifts to different adaptive zones, etc. For this reason, and although it has the advantage over many other criteria of being objective and nonarbitrary (at least in the form advocated by SIBLEY & AHLQUIST, 1982), it is my opinion that this criterion should not be used to determine the ranks of taxa. On the other hand, the " genetic " distance between species measured by the very sensitive criterion of DNA hybridization is obviously of a very great interest to determine the phylogenetic relations between species, for the study of the rates of evolution, etc.

VAN VALENS's metataxinomic criterion

A simple criterion of comparison of classifications is the number of species and of higher taxa of every category in the group under study. Such a criterion would allow one to uncover disparities between groups: thus, if one compares the " mean " family of insects to the " mean " family of mammals, one notices that the first one contains many more species than the second one ; the difference is less important for the number of genera (VAN VALEN, 1973: 333). Like some ecological criteria mentioned above, a criterion of this type would roughly measure the " ecological success " of a group. However the meaning of the number of taxa taken by itself is not clear, since various factors interfere with this number: the size of species, the " width " of the adaptive zone occupied by the group, the presence or absence of other animal groups in this zone, etc. The criterion cannot therefore be used to standardize the classification of different groups, although this has been contemplated and even put into practice by some systematists having an empirical conception of classification.

Although such criteria cannot be used to construct a classification, they allow one on the other hand to compare classifications between themselves. Several authors have already addressed this question and produced quantitative analyses of zoological classifications (WILLIAMS, 1951; MANDELBROT, 1956; MAYR & SHORT, 1970; CLAYTON, 1972; VAN VALEN, 1973; GORHAM, 1977; BOCK & FARRAND, 1980; STOYAN, STOYAN & FIKSEL, 1983). In this respect, the most interesting analysis seems to be VAN VALEN's (1973). This author proposed a new criterion, which he called " metataxinomic criterion ", to analyse biological classifications and ascertain whether categories occupy similar " positions " in the classification from one group to another. The " position " of every category is determined, for every group, by the number of taxa belonging to the category, in relation to the total number of species of the group (for more clarity and details, see table II, fig. 2 and their legends). As shown in fig. 2 and as will be discussed in more detail below, according to this criterion some classifications may be described as "balanced ", others as " oversplit " and others as " overlumped ". The meaning of these differences is not clear, however VAN VALEN (1973: 341) notes:

> " Although there is no apparent reason other than symmetry why categories should tend to be equally spaced, it is interesting that the two most studied groups of animals, the Chordata and Insecta, approach equal spacing more closely than any other major taxa except perhaps the Platyhelminthes and Protozoa."

One may suppose that, when this criterion is applied to groups which are important enough (phyla containing thousands of species and of higher taxa), the overall result " erases " the disparities which may exist at a lower scale as to the " quality " of the current classification (groups having been the subject of more or less recent revisions, by authors with a tendency toward splitting or lumping, in favor of such theory of classification, etc.), and expresses in a synthetic way the particularities of the classification studied, allowing therefore comparisons. It would thus be a good criterion of " comparative systematics ".

VAN VALEN's metataxinomic criterion is therefore interesting for it allows one to compare classifications and possibly to draw conclusions as to either the validity of a classification, or the

Source : MNHN, Paris

evolutionary modalities within a group (see below), but it does not in itself make definition of taxa possible, nor does it make them equivalent from one group to another. It could permit one to do it within the frame of a totally empirical conception of classification, in which the only objective would be to build the most " practical " possible system of identification: in such a perspective, it would be necessary to modify the existing classifications at any price in order to make them as " balanced " or "symmetrical " as possible, a classification wherein all categories would be equidistant being the richest in information contents. On the contrary, within the frame of an evolutionary conception of systematics, it is interesting to observe disparities in the classification from one group to another, for they may indicate the existence of different evolutionary phenomena: we shall come back to this problem below.

Hybridizability criterion

As finally concerns the criterion of hybridization, VAN VALEN (1973: 334) believes that it cannot be retained as a criterion permitting one to make taxa equivalent from one group to another:

> " Because it is affected by sympatry, is possible only for low categories, and can be oligogenic or even monogenic, it does not seem to be a good estimator. "

Furthermore he thinks that this criterion is probably equivalent to the criterion of "genotypic diversity " discussed above: by so doing he ignores the difference between structural and regulatory genes on which the present work insists.

Other authors have also considered that interspecific hybridization could not give useful information for constructing supraspecific classification, because of the variability of the results of the hybridization between species considered very close along other criteria, of the disparities observed between reciprocal crosses, and generally of the poor correlation between the results of hybridization and the current classification (see e.g.: MONTALENTI, 1938; MOORE, 1955; COUSIN, 1967). These authors have not realized that the negative results of hybridization do not have the same value as the positive ones.

On the other hand, the argumentation here presented relies upon the very particular meaning that is attributed to the success of hybridization. According to this interpretation, the criterion of hybridizability has a deep synthetic biological meaning, which largely exceeds the meaning of every morphological, molecular, ecological, or other, criterion taken individually. In the light of this criterion, the genus stops being an artificial category to become, in the same way as the species, an evolutionary systematics category, expressing the existence of real evolutionary phenomena in nature. The groups thus defined are equivalent, in functional genetic terms, to one another. Within each of these " genetic units ", the variance of the systems of genetic regulation remains moderate enough to allow the preservation of a possibility of hybrid development between two elements of this unit.

Therefore the hybridizability criterion allows one to recognize real taxa (defined by a relational, objective and nonarbitrary criterion) which are equivalent between them from one group to another. Such criteria being rare, it is important to use this one well, and to define its use in order to make it the most general possible at the scale of the whole animal kingdom. In this respect, two aspects of my proposition may be discussed in a more detailed way: (1) the choice of the developmental stage retained for considering that the hybridization between two species has succeeded; (2) the decision to assign the rank of genus to the taxon defined by this criterion of hybridizability.

Choice of the developmental stage

In order to decide that the hybridization between two species has " succeeded ", one must dispose of a stage of reference, the minimum stage to be attained by the hybrid product. In this respect , VAN GELDER's (1977) proposition slightly differs from mine, since this author suggested the criterion of " birth of a living offspring ", while I suggested that of " obtaining of a viable adult hybrid " (DUBOIS, 1981 a). This last criterion seems to me to merit retention, for

Source : MNHN, Paris

it has a larger generality in the whole animal kingdom than that of birth. Virtually all animal species (except maybe some Protozoa) possess an adult stage, characterized by sexual maturity and the ability to reproduce, and differing in that from the stages which precede it (embryo, larva, young, subadult, etc.). The latter have no generality, not any more than the stages of birth, of hatching, of metamorphosis, etc., which can occur at very different moments of development from one group to another. The notion of " birth ", as used by VAN GELDER (1977), is valid only for mammals and other viviparous animals.

In most animals, if the adult stage is *defined* by the acquisition of sexual maturity and by the ability to reproduce, this stage may be *recognized* by many other characters (size, morphology, behavior). This allows the use of this criterion even in the case of infertile hybrids, which are admittedly unable to reproduce but which have nevertheless reached the adult stage of development, which, for the reasons given above, is enough in my opinion to consider a hybridization as " successful ".

As concerns mammals, experience shows that a number of hybrids which reach the stage of birth alive later have a more or less normal growth and usually live until the adult stage: from a purely practical point of view, the application of the criterion of the viable adult would entail virtually no difference as compared with VAN GELDER's (1977) criterion of the living newborn offspring.

Choice of the taxinomic rank

TURESSON's (1922) concept of *coenospecies* and its synonyms (see BERNARDI, 1980), among which is the *syngameon* in the sense of CUÉNOT & TÉTRY (1951) but not of LOTSY (1918), applies to a group of species liable to give viable hybrids in the laboratory, be they able or not to do so in nature.

The few authors who have until now made use of the word coenospecies (or of its synonyms) used to designate by this term a group of species devoid of taxinomic meaning: for them, the coenospecies sometimes included several genera, while in other cases several distinct coenospecies were maintained in the same genus.

On the other hand, the above propositions amount to saying that it would be good, because of the great biological meaning of the nontaxinomic category of coenospecies, to make the latter coincide with the taxinomic category of genus. The choice of this latter category could be discussed. One could contemplate the possibility of making the coenospecies coincide either with a lower (subgenus) or with a higher (tribe, subfamily, or even family) category than the genus. In a few cases, such a proposal would have the advantage of entailing less taxinomic disruptions: thus in birds, where, as we shall see, the application of this criterion would considerably modify the generic (and, by way of consequence, familial and ordinal) classification, it would appear justified to make the coenospecies coincide with the family, which would much less modify the current classification. But, the objective of my proposition being to standardize systematics in different groups, what would be " gained " on the side of birds, would be " lost " in all other groups, where it would be necessary to rise genera to the rank of families: eventually, the disruption would be the same or even greater, but it would concern other groups than birds.

The choice of the category genus for the coenospecies was imposed on me, so to speak, by a set of reasons. First of all, an intuitive one. The genus is the first important higher category, and it seems logical to place at this level the first important break above the species: species are genetic pools protected from each other, genera genetic units definitively isolated from each other, but within which, at least in artificial conditions, exchanges and relations may exist. It is also what has been felt by all the other authors who have proposed the use of a hybridizability criterion in supraspecific systematics (SIMPSON, 1961; VAN GELDER, 1977; PLATEAUX, 1981): they all suggested the use of the genus, not the family or another category, for grouping together hybridizable species.

Furthermore, it so happens that the choice of this category modifies relatively little, except in exceptional cases like birds, the generic classification of many groups, as if this criterion had already been more or less unconsciously used by systematists since long ago. In fact the genus so defined generally coincides well with the genus that the other " synthetic " criteria mentioned above, in particular the " ecological " criterion (INGER, 1958), recognize. Actually, it is this

Source : MNHN, Paris

agreement which first drew my attention and led me to formulate the concept of geniation (see below).

Let me finally note that the use of the hybridizability criterion at the level of the genus category will give rather balanced results in the light of VAN VALEN's metataxinomic criterion, as dicussed below, while if the coenospecies was to coincide with a higher category like that of family, this would lead to an important imbalance in classifications, according to this criterion.

THE HYBRIDIZABILITY CRITERION AND THE CLASSIFICATION OF THE VERTEBRATA GNATHOSTOMATA

INTRODUCTION

VAN VALEN's (1973) metataxinomic criterion was presented above. The application of this criterion to the current classifications of the six classes of Vertebrata Gnathostomata (Table II, fig. 2) allows one to disclose the existence of three types of classifications (DUBOIS, 1988):

(1) a " balanced " or " symmetric " pattern, in which the major categories of the Linnaean hierarchy (species, genus, family, order, class) are roughly equidistant: only the smallest class of Gnathostomata, that of Chondrichthyes, currently has a classification of this type;

(2) an " overlumped " pattern, in which the taxa of the intermediate categories (genus, family, order) are " not numerous enough ", at least according to the scale of the metataxinomic criterion: such a classification is observed for amphibians and partially (only for the higher categories, but not at the level of the genus) for reptiles;

(3) an " oversplit " pattern, in which the taxa of the intermediate categories are " too numerous " according to this criterion: the three classes Osteichthyes, Aves and Mammalia present classifications of this type.

As was remarked above, the meaning of the " balanced " or " unbalanced " pattern, according to this criterion, of the classification of a group is far from being clear, but one may at first contemplate two factors which may be responsible for an unbalanced classification: (1) mistakes in the building of the classification (wrong weighing of characters, lack of information, etc.); (2) particularities proper to the mode of evolution of the group studied.

The confrontation of VAN VALEN's metataxinomic criterion with the hybridizability criterion in the whole group of Vertebrata Gnathostomata may bring us additional information in this field.

It is thus striking to observe that the three classes which appear " oversplit " according to VAN VALEN's metataxinomic criterion (Osteichthyes, Aves, Mammalia) are precisely those which have the highest rate of " intergeneric hybrids ", and therefore in which the application of the hybridizability criterion would reduce the most the number of genera and, by way of consequence, of other higher taxa.

AMPHIBIANS AND REPTILES

In amphibians almost all hybridizations liable to give viable adults known until now (MONTALENTI, 1938; MOORE, 1955; BLAIR, 1972 b; etc.) occur between species which are traditionally classed in the same genus. Only two examples of " intergeneric " hybridizations in this class have

Source : MNHN, Paris

been known until now: between the " genera " *Hyla* and *Pseudacris* (RALIN, 1970) and between the " genera " *Pleurodeles* and *Tylototriton* (FERRIER, BEETSCHEN & JAYLET, 1971). In both cases the fact of merging both genera, while conserving the name of the second one as subgenus of the first one (DUBOIS, 1982 a, 1984 b), does not raise any particular problem, and even throws a new light on the phylogenetic relations within these groups. At the level of the classification of the whole class of amphibians, these modifications have virtually no effect.

The same is essentially true for reptiles, where until now no adult hybrid is known which appears as " intergeneric " according to the current classification (MERTENS, 1950, 1956, 1964, 1968, 1972; ARNOLD, 1973; etc.).

Now, according to VAN VALEN's metataxinomic criterion, the classifications of amphibians and reptiles appear to be not very far from a " balanced " or " symmetric " type. At the level of the genus, reptiles appear a little oversplit, and at the other levels, a little overlumped; amphibians appear a little overlumped at the levels of genus and of family, and much overlumped at the level of the order. It is therefore " logical ", if both criteria are congruent, that the hybridizability criterion could be applied without leading to an appreciable reduction in the number of genera, or of higher taxa.

BONY FISHES

The situation is very different for the classes of Osteichthyes, Aves and Mammalia: "intergeneric " hybrids are numerous in these groups, and the grouping together of genera which the use of the hybridizability criterion would require, would probably have to be followed by a grouping together of families and other higher taxa, for otherwise many suprageneric taxa would become monogeneric or almost so.

In bony fishes, the potential " intergeneric " hybrids are numerous (MOENKHAUS, 1910; HUBBS, 1955; MCALLISTER & COAD, 1978; DAGET, 1983). A finer analysis shows that these hybrids are much more abundant in freshwater fishes than in marine fishes (HUBBS, 1955; DAGET, 1983), which can be partially accounted for by the fundamental disparities between both types of environments, in particular in terms of diversity and stability (HUBBS, 1955), and by the fact that both groups certainly show important differences in their mechanisms of speciation,

> " which result mainly, in continental waters, from positional isolation and from the splitting up of ecological niches, while, in marine waters, they are mainly based on reproductive isolation. " (DAGET, 1983: 401; translation mine).

MAMMALS

In mammals also, potential " intergeneric " hybrids are numerous (GRAY, 1972). VAN GELDER (1977, 1978) has undertaken a revision of the generic classification of this group basing himself on the criterion described above (an hybridization is considered " successful " when it gives at least one viable newborn offspring). At the moment, these works have led him to downgrade 44 names of genera of mammals to the rank of subgenera or even of synonyms of other generic names. With this operation, the number of genera of mammals comes down from 1004 (according to ANDERSON & JONES, 1976) to 960. The consequence of this reduction within the framework of VAN VALEN's metataxinomic criterion is shown in fig. 2: although it tends to lower the difference between the value observed for the position of the category genus and the " expected " value in the case of a balanced classification, this reduction is slight and the mammals remain

Source : MNHN, Paris

appreciably oversplit even after this action. Three explanations of this phenomenon may be suggested, which are probably all partially valid:

(1) There remains certainly other cases of potential " intergeneric hybridization " in mammals, which were not yet known at the time of VAN GELDER's (1977, 1978) reviews. In particular it is likely that artificial hybridizations, in conditions allowing one to avoid the pre-ejaculatory and post-ejaculatory mechanisms of isolation (artificial fertilization and *in vitro* culture of the embryo in particular) will allow the discovery of many other potential " intergeneric " hybridizations in mammals. When these are taken into account, the number of genera of this class will keep on decreasing.

(2) As we have seen above, the criterion of hybridizability is only one of the criteria which may be used to recognize genera as genetic, phylogenetic and ecological units. In the light of these various criteria, it is likely that the number of genera of mammals would decrease even more.

(3) As we have also seen, there is at the moment no serious reason to believe that a " balanced " or " symmetric " classification according to VAN VALEN's metataxinomic criterion would be " better " or " more natural " than another one. On the contrary, a departure from this " balanced " pattern may correspond to a reality, and be the indication of the existence of certain particularities proper to the group studied. It may in particular express the fact that the characteristics of the evolution of this group are atypical as compared to those of the related groups. As concerns mammals, evidence exists that the group has experienced a particularly rapid evolution of the systems of genetic regulation, of morphology, of karyology, and of the loss of the ability to hybridize between related species (MAXSON, SARICH & WILSON, 1973; WILSON, MAXSON & SARICH, 1974; WILSON, SARICH & MAXSON, 1974; KING & WILSON, 1975; WILSON, 1975; WILSON *et al.*, 1977; WILSON, CARLSON & WHITE, 1977; CHERRY, CASE & WILSON, 1978; CHERRY *et al.*, 1979, 1982; BENGTSSON, 1980; LARSON, PRAGER & WILSON, 1984; etc.). It is therefore likely that the " oversplit " pattern of the supraspecific classification of this group corresponds at least in part to the reality.

This example allows one to sense in concrete terms the interest of the use of standardization criteria, like the hybridization criterion: the fact that, even after the use of this criterion (and of other synthetic ones), the classification of a group remains " atypical " as compared to the " mean " or " balanced " classification, or to the classifications of neighboring groups, will be liable to draw the attention on particularities proper to the evolution of this group, and to stimulate research on the evolutionary mechanisms responsible for these disparities. This will not be possible if one does not possess any criterion allowing one to refer all classifications to a common yardstick.

BIRDS

The classification of birds will give us a negative example confirming this interpretation. The number of " intergeneric hybrids " in this class is extremely high (GRAY, 1958; PRAGER & WILSON, 1975; MILSTEIN, 1979; etc.). The use of the hybridizability criterion would entail a radical change in the systematics of this class, and particularly of some of its families, like that of Anatidae (JOHNSGARD, 1960), where the number of " intergeneric " hybrids is very high. Would such a modification be disastrous, as certain ornithologists seem to believe, or would it correspond to a real need?

The fact that, as compared to other groups, the classification of birds is much oversplit, has already been emphasized on several occasions (see e.g.: SIBLEY, 1957; CROWSON, 1970; PRAGER & WILSON, 1975; BOCK & FARRAND, 1980; DUBOIS, 1982 a ; SIBLEY & AHLQUIST, 1982; PASTEUR, 1985). A noticeable effort of reduction in the number of supraspecific taxa of this class, which was extremely high at the beginning of the

Source : MNHN, Paris

century, has already been made by ornithologists. The fact remains that the current classification is much oversplit, and in particular that the number of genera is much too high, as was specially emphasized by CROWSON (1970):

> " We cannot help feeling that students of birds and of moths would be better zoologists and better systematists if, despite the difficulties, they seriously tried to observe and appreciate the generic characters in their animals. " (CROWSON, 1970: 51).

It is interesting to observe that numerous are the ornithologists who, reporting upon the discovery of natural hybrids or the obtention of artificial hybrids between species of birds classed in different genera, expressed some doubts as to the validity of the separation of these genera. However, with the help of the strength of tradition, they generally merely formulated these doubts in the Discussion of their work, without going so far as to group together the species of both genera in a single one, as may be illustrated, without any concern for exhaustivity, by the following citations drawn from papers dealing with " intergeneric " hybrid birds:

> " That these two species should be considered members of different genera, in the light of the present evidence, seems open to question. " (WILLIAMSON, 1957: 122).
>
> " a serious study of the generic limits in the Trochilidae is in order. " (BANKS & JOHNSON, 1961: 26).
>
> " The discovery of this new intergeneric North American hybrid hummingbird combination (...) lends additional support to the oft-expressed view (...) that the time is ripe for a thorough study of the generic limits within the Trochilidae. " (LYNCH & AMES, 1970: 212).
>
> " The existence of the hybrid, and its mating with *T. verticalis*, emphasize the close relationship between *T. verticalis* and *M. forficata* and support the proposal advanced by SMITH (...) that *M. forficata* be placed in the genus *Tyrannus*. " (DAVIS & WEBSTER, 1970: 42).
>
> " it is clearly apparent that serious consideration should be given to merging the genera *Lophortyx* and *Callipepla* with *Colinus*." (JOHNSGARD, 1970: 87).
>
> " Because of the general morphological similarity of swallows, MAYR and BOND (...) questioned the reality of generic limits in this family and suggested that grounds for separating *Petrochelidon* from *Hirundo* were particularly weak. The occurrence of hybridization between *Hirundo* and *Petrochelidon* and the biochemical evidence of close genic similarity between *H. rustica* and *P. fulva* strongly support this view-point. " (MARTIN & SELANDER, 1975: 364).

One may wonder why the classification of birds is so oversplit. One reason is certainly the fact that this class has been the subject of a very high number of works: as a matter of fact it is very frequent that very well known groups are excessively divided as compared to the less studied neighbouring groups (see in this respect CROWSON, 1970: 48-49). On the other hand many genera of birds, in particular among diurnal species, " rest " on characters of the plumage, and often of the plumage of the males only. The importance attributed by systematists to these characters is certainly in relation with the fact that these are very visible, sometimes spectacular, characters, and that man, a species in which sight is more developed than the other senses, tends to give greater importance to characters accessible to this sense than to others.

During the round table of the French Zoological Society on " Genus, subgenus and species-group " (Paris, 14 March 1978), Philippe DREUX insisted upon the fact that the systematics of birds would certainly be much less divided if abstraction had been made of the feathers to build it. Concerning pheasants, among which the known " intergeneric " hybrids are numerous (see GRAY, 1958), he humorously summarized this observation: " Pluck them, and no one will recognize them, even by their taste! " (DUBOIS, 1982 a: 32).

The evolutionary meaning of the important differences in the plumage of males which is

Source : MNHN, Paris

often observed between species of diurnal birds, which are in other respects very close, is very clear: these are pre-ejaculatory mechanisms of isolation allowing the avoidance of the hybridization of these species in sympatry. These are therefore characters related to *speciation*, not characters expressing a more important divergence. The rôle played by the differences of plumage (and also of mating call, of nuptial parade, etc.), in diurnal birds is played by other characters in other groups of animals. Thus in anuran amphibians the mating call of males plays a fundamental rôle in the pre-ejaculatory isolation between species: in these animals it is frequent to encounter species morphologically identical or very similar but having very different mating calls. A classification of anurans which would give mating calls an exaggerated importance, comparable to that sometimes given plumage characters by ornithologists, could lead to classifying these species in different genera. The same would be true with a classification of micromammals which would give a great importance to olfactory criteria.

We are indebted to SIBLEY (1957) for an interesting paper where ideas close to the preceding ones are expressed in a more detailed way, and where this author most justly writes:

> " The high incidence of monotypic genera in groups of sexually dimorphic visual animals is due to erroneous human evaluation of the taxonomic value of signal characters. Morphological structures evolved under the selection pressure of deleterious hybridization and/or sexual selection seem highly ' specialized ' to the intelligent discrimination of the human taxonomist who therefore accords them generic rank on a ' degree of difference ' basis. This is a coincidental result of the fact that we too are visual animals and hence can and do utilize visible characters in taxonomy. It is significant that ' intergeneric ' hybrids are found almost exclusively in visual animals, principally birds and, to some extent, fish. It is apparent that genera in such groups should not be based only upon secondary sexual characters nor upon characters which have been reinforced by selection against hybrids since these, inevitably, are *species* characters. " (SIBLEY, 1957: 187).

It seems therefore that the reduction of the number of genera of birds which would be entailed by the use of the hybridization criterion proposed above would be a salutory operation: genera thus defined would have much more biological meaning than the numerous monospecific genera which are currently based on plumage characters or on other characters expressing a simple divergence between sympatric related species. It is likely that the reduction in the number of genera of birds, if it was accepted by ornithologists, would be followed by an important reduction in the number of families and orders of this class. Moreover, the whole current classification of birds seems still susceptible of important modifications, despite the numerous works which have already been devoted to it. It is in particular possible that such modifications become necessary as a result of the reassessment which seems to be necessary of some aspects of the phylogeny of this group (see CRACRAFT, 1972).

In recent years very interesting works have been devoted to studies of the molecular evolution of birds, and have led to the rather surprising conclusion that divergence, at the level of the structure of proteins, between lower taxa of birds is extremely weak as compared to the divergence which exists between numerous other vertebrates of similar taxinomic levels (see e.g.: PRAGER *et al.*, 1974; AVISE & AQUADRO, 1982; AQUADRO & AVISE, 1982; AVISE, 1983; PASTEUR, 1985; VIOT, 1985); it is similarly so for the divergence at the level of the sequence of mitochondrial DNA (KESSLER & AVISE, 1985). Several hypotheses have been put forward to account for these observations, among which the most often mentioned and discussed (see e.g.: ZINK, 1982; AVISE, 1983; KESSLER & AVISE, 1985) are the two following ones: (1) the taxa of birds studied would have a more recent origin than the taxa of the other groups; (2) molecular evolution would be slowed down in birds as compared to other vertebrates:

> " One possibility is that protein evolution is decelerated in birds: the protein ' clock ' may tick at a slower pace." (AVISE, PATTON & AQUADRO, 1980: 303).

Source : MNHN, Paris

A third hypothesis, which also deserves consideration (AVISE & AQUADRO, 1982; SIBLEY & AHLQUIST, 1982; VIOT, 1985), is precisely that according to which the supraspecific classification of birds is oversplit.

Once again, we here face the *practical* interest of having a criterion of standardization like the hybridizability criterion: in the absence of such a criterion, it remains rather gratuitous to discuss the possible acceleration or deceleration of the molecular evolution rate in an animal group. This was well emphasized for example by SIBLEY & AHLQUIST (1982), who strongly feel the necessity of such a criterion of standardization of the different classifications. Unfortunately, the criterion proposed by these authors (the age of taxa, as it may be estimated by DNA hybridization) is not able to play this rôle well, for the reasons detailed above.

As we have seen, according to VAN VALEN's metataxinomic criterion, the current classification of birds appears to be "oversplit", which supports the preceding remarks. It would be most interesting to construct, at least for information only, a new supraspecific classification of birds where would be grouped together two by two all the genera with two species at least being liable to hybridize, then where the number of families and orders would be reduced according to these groupings. Upon examination of the lists of hybrids of birds (GRAY, 1958) and of mammals (GRAY, 1972) currently known, it is clear that the reduction in the number of genera entailed by the use of the criterion of hybridizability would be much more drastic in the former than in the latter. The classification of birds would become, after such an operation, certainly much closer to a "balanced" classification according to VAN VALEN's metataxinomic criterion than that of mammals after the lumpings of genera realized by VAN GELDER (1977, 1978) (see Table II and fig. 2). Then, it would be possible to validly test the hypotheses mentioned above on the differences between the evolutionary rates of the systems of genetic regulation between different groups.

CRITICAL STUDY OF THE USE OF THE HYBRIDIZABILITY CRITERION TO DEFINE GENERA

Several arguments can be put forward for or against the use of the above defined criterion to group together species in a same genus. Some of these were already discussed above. Some others remain, which we shall now examine.

SOME ARGUMENTS AGAINST THE USE OF THIS CRITERION

(1) A first argument consists in saying that this criterion cannot always be used. In certain cases, it cannot be used because of intrinsic properties of the compared species: thus the criterion cannot be used in paleontology, nor for living species with uniparental reproduction (species with a true asexual reproduction; species with uniparental reproduction derived from biparental sexual reproduction: autofertilization, parthenogenesis, etc.). In other cases, the criterion cannot be used for purely material reasons: in many groups of animals, breeding is difficult, artificial insemination cannot be achieved as easily as in amphibians or echinoderms, and it is therefore very difficult or impossible to study hybridization in the laboratory.

In reality an argument of this type could be used against most of the methods used in systematics. In modern systematics data are used which come from morphology, anatomy, bio-

Source : MNHN, Paris

chemistry, karyology, ecology, behaviour, bioacoustics, parasitology, etc. It is quite rare that all these data should be available for a given group and, in paleontology, the only available data are those derived from the study of the fossilized parts of animals. However no author has ever suggested, at least let us hope so, to use in systematics only the method which is the smallest common denominator to all possible studied, and ever proposed to base all animal systematics on the study of the sole fossilizable parts! Systematics make use of the highest possible quantity of information concerning living beings. In certain cases the information is rich, in others it is less so, but it is always desirable to have as much information as possible. The criterion of hybridizability can certainly not be used in all cases, but this does not forbid its use when it is possible.

Furthermore, one may hope that in some of the groups where this criterion cannot be used at the moment for simple material reasons, the progress in our knowledge of the biology of these animals (including in particular the achievement of breeding and of artificial insemination) will in the future allow us to use it.

As concerns the species with uniparental reproduction, everything depends on their more or less isolated or exceptional nature. When only a few species are concerned, e.g. with parthenogenetic reproduction, within a vast group most of the species of which still use sexual reproduction, analogies with the latter will sometimes help in building up the classification, including at the generic level. On the other hand, in groups where the rule is uniparental reproduction, as e.g. bdelloid rotifers (De Beauchamp, 1965), such a resort to analogy is hardly possible and one must admit not to be able to define genera by using, even in an indirect way, the criterion here proposed.

(2) This criterion may be blamed for its asymmetry: it only takes into account the positive results of hybridization and can therefore be used to group species together within a genus, not to separate genera.

Such an asymmetry is the fact of many other criteria of current use in systematics. To give only one example, one of the criteria which may be used to ascertain that two different populations belong to two distinct species is based on the fact that hybridization between individuals of these two populations is impossible or always leads to a failure of development. In this case an absolute genetic isolation exists between both populations, and by definition these cannot belong to the same species. On the other hand the reverse result does not at all allow one to draw the reverse conclusion. The ability of two populations to give birth to hybrids between them, even sometimes in nature, does not at all imply that they belong to the same species. Hybrids may occur in nature sometimes in the zone of hybridization between two subspecies of a same species, sometimes in the zone of overlaping and hybridization between two prospecies of a same superspecies, and finally sometimes as isolated hybrid individuals, in a zone of wide sympatry between two good species. In all these cases, what will allow one to choose between these different possibilities are arguments other than the simple presence of hybrids (see e.g. Dubois, 1977 b; Bernardi, 1980). This is here also an asymmetrical criterion, which does not prevent it from being very useful where it can be used.

(3) Another objection to the use of this criterion is that its adoption would entail important modifications in the systematics of certain groups. The importance of these changes would be extremely variable according to the group considered, as was shown above by the examples taken in the vertebrates. I discussed in a relatively detailed manner the problem of the birds, because this class is probably the one where is posed with the highest acuteness the problem of the disruption of the classification consecutive to the application of the new criterion. The arguments developed above, or other similar ones, are also applicable to other groups, where " intergeneric " hybrids are numerous.

Be that as it may, it is not exceptionally that the introduction of new arguments entails modifications in the systematics of a group, and these arguments cannot be rejected under the sole pretext of " preserving the stability of nomenclature ". The stability of nomenclature and of classification is certainly desirable in general, as long as new information does not contradict the tradition, but it should not be a brake on the improvement of systematics which is sometimes

Source : MNHN, Paris

demanded by the progress of our knowledge of the living beings.

As concerns the groups, like birds, where the application of the criterion of hybridizability would lead to important changes at the generic level, it might be advisable, at least as a provisional measure, to conserve the very well known generic names as subgeneric names.

While the above discussions are mainly based on purely formal arguments and for this reason seem to me of little importance, the last two objections which I will consider touch on real biological problems and are more interesting. In the current state of our knowledge, they do not seem to prove justified, but we must nevertheless examine them.

(4) The first objection bears on the interpretation which I have adopted here of the genetic meaning of the success of the hybridization between two species. Following other authors (WHITT, CHILDERS & CHO, 1973; WILSON, MAXSON & SARICH, 1974; WHITT, PHILIPP & CHILDERS, 1977; WILSON, CARLSON & WHITE, 1977; OLIVER, 1979; PHILIPP, PARKER & WHITT, 1983; PARKER, PHILIPP & WHITT, 1985 a, 1985 b; etc.), I have here admitted that the success of the development of a hybrid until the adult stage expresses a strong similarity and a compatibility of the systems of genetic regulation of the two hybridized species. Another interpretation could be considered: that according to which only one of the two systems of genetic regulation present in the hybrid would in fact be active. If it so happened that the genome of one of the two species was totally inactivated (repressed) in the hybrid, the latter would correspond from the viewpoint of its active genetic material to a haploid or parthenogenetic individual, and the criterion of hybridizability would lose the fundamental biological meaning which was attributed to it here.

The known facts do not seem at all to support this hypothesis. In some hybridizations between relatively distant species, evidence exists that certain structural genes of one or the other of both parental stocks are inactive, because of phenomena of *repression*, but the repression on one hand only touches a limited proportion of genes, and on the other hand concerns sometimes the maternal, and sometimes the paternal alleles (see e.g. WHITT, CHILDERS & CHO, 1973), which indicates that both genomes take part, at least partially, in the ontogenesis. In the case of the inactivation of the genes situated on one of the two X chromosomes of mammals, the study of certain hybrids, some Canidae and some Equidae, shows that it is sometimes the maternal X, and sometimes the paternal X which is inactivated (SEROV, ZAKIJAN & KULICHKOV, 1978 a, 1978 b). Discussing the results of a study bearing on hybrids of teleosts, WHITT, CHILDERS & CHO (1973: 59) write:

> " These results and those of previously published studies support the postulate that there is a positive correlation between the evolutionary distance of the parental genomes and the extent of allelic repression in the F1 hybrid. "

Thus, in the hybrids between very close species, there may exist no allelic repression at all (see e.g. CHAMPION & WHITT, 1976). On the other hand, it seems that when the divergence between the two genomes becomes too great, rather than a complete repression of one of the two and a " normal " development due to a single genome, what occurs is a failure of development. It will be important in this respect to follow the future works on genic expression in hybrids, but in the current state of knowledge this objection does not seem to be relevant.

(5) The last objection is the following one: might not the use of this criterion lead to the grouping together in a same genus of organisms liable to hybridize step by step and constituting a " chain ", so to speak, the extreme links of which would be extremely dissimilar? Such a situation would occur if hybridization was a success between A and B, then between B and C, between C and D, and so forth without interruption. If this was the case, the whole classification might come apart like knitting, to lead to the maintenance of only a few genera within each great group!

In front of this theoretical hypothesis, only experience can answer. Now, the examination of lists of species liable to give between them adult viable hybrids (thus, in the vertebrates: SUCHE-

Source : MNHN, Paris

TET, 1897; MONTALENTI, 1938; MERTENS, 1950, 1956, 1964, 1968, 1972; HUBBS, 1955; MOORE, 1955; GRAY, 1958, 1972; BLAIR, 1972 b) shows that successful hybridizations allow one in reality to define relatively small hermetic groups, separated from other similar groups by discontinuities, and not open chains. Therefore, by calling upon this criterion, it would appear that genera are closed communities, natural units, just like species, although in a different manner.

SOME PRACTICAL ARGUMENTS IN FAVOR OF THE USE OF THIS CRITERION

The use of the hybridizability criterion to group species together in a same genus is of great theoretical and practical interest.

I already discussed at length the theoretical aspects of this question. A few purely practical arguments in favor of the use of this criterion must also be mentioned.

(1) Genera recognized according to this criterion will probably be a little larger on the average than they are currently, i.e. they will include a higher average number of species. In many groups, where the excessive number of genera has already been emphasized by many authors (e.g. MAYR, 1943; ROSEN & BAILEY, 1963; CROWSON, 1970), such a change would be most welcome:

> " The desirable trend now would be to reduce large numbers of currently accepted genera to the level of subgenera or even species-groups (...), and at least the idealists among us may hope that a change so clearly in the interests of the scientific majority is almost bound to come about. " (CROWSON, 1970: 298).

(2) Although this criterion has already been mentioned by some authors and used in a few cases, no systematic attempt to use it to redefine genera within a given group has so far been made, except for that of VAN GELDER (1977, 1978) in mammals. As we have seen, the changes that such an operation would bring would be of a very variable scope from one group to another, e.g. very limited in amphibians and very great in birds, which is certainly not liable, despite the arguments in favor of this proposal presented above, to lead specialists of groups like birds to be enthusiastic about it! However it must be insisted upon that the taxinomic disruption would occur *once and for all* and that, once it has occurred, the generic nomenclature of the group would be *very much stabilized*. The hybridizability criterion, if it is used appropriately, avoiding the few pitfalls pointed out above, is a "definitive " criterion, which will never have to be reconsidered later: two species liable to give viable adult hybrids will remain in the same genus, independently of all other arguments concerning their morphology, their biology, etc. For many cases in all the groups where generic status is currently a matter of discussion but where viable adult hybrids do exist, such a stabilization will be welcome: it will stop nomenclatural comings and goings between several generic names for a given species. Despite an important initial disruption in some groups, the use of this criterion would in the long run have a strong stabilizing effect on generic classification and nomenclature in zoology.

(3) This criterion is of a relatively easy and " economical " use, since the discovery of a single hybridizable pair may lead to the merging of two genera even if these contain a much higher number of species.

(4) Finally, while in some groups the use of this criterion is difficult for material reasons, in other ones it is easier than long morphological, molecular, ecological analyses. In some groups where the studies of these last types are progressing slowly, the use of this criterion should contribute to a rapid stabilization of the generic nomenclature, while allowing of course the continuation of more detailed studies on the other aspects.

Source : MNHN, Paris

The criteria of the genus

As was emphasized by Crowson (1970: 48-49), the specialists of a particular group, who know it well and appreciate all its subtleties, often tend to give it a greater importance and to subdivide it to the maximum, to recognize in it many hierarchized subgroups, and often later to elevate the ranks of the latter (as compared to the neighbouring groups which have been the subject of less detailed works). It is important always to try to put " one's " group back in the general context, to allow as much as possible classification to play its universal information rôle. The principles and criteria discussed above may be somewhat useful in this respect.

I insisted particularly on the hybridizability criterion, because it is new and its application would be followed by appreciable modifications in the current classification of many groups. However, it is clear that this criterion cannot, and must not, be used alone to identify genera and build up classifications. It must be used within the framework of the " synthetic concept " of the genus as it has been characterized above, and in conjunction with the other criteria available within this framework. By the way, several of these criteria have already been used for a long time by many systematists.

As has been shown elsewhere (Dubois, 1977 b), there exists a certain hierarchy among the criteria which allow one to decide if two sets of populations are or not distinct species, some criteria being more important, more conclusive than others:

> " The species concept (protected gene pool) is a synthetic concept and in this field the use of a single criterion is often not enough to reach definite conclusions. However, the joint consideration of several characters (...) often allows one to remove difficulties. It is particularly important to dispose of data on several *independent* characters, and to ascertain whether they reach similar conclusions or not. In practice it is this joint use of several independent characters which permits, in many cases, decision. It is thus in general useless, from a practical point of view, to dispose of data on a high number of characters. The combinations of characters which may be used are very diverse and it is not useful here to give examples. However there exists a certain hierarchy among criteria, which may be briefly summarized as follows.
>
> The criterion of genetic compatibility (which may be demonstrated, or deduced from other considerations, e.g. from karyology) is indeniably the surest criterion of the existence of two species (apart from the reservations made above on this question). In the cases of genetic compatibility, it will first be necessary to study the spacio-temporal relationships between both forms, and to ascertain whether they are sym-, para- or allopatric (or -chronic). In sympatry, all the criteria showing a marked discontinuity between both groups can be used to indicate that two separate gene pools do exist; it will be valuable in this case to use independent criteria (morphology of adults and larvae, mating calls, biochemistry, ecology, etc.). In parapatry, the study of the detailed distribution of both forms, of the hybridization and introgression in the contact zones take a particular importance. In allopatry, the joint examination of various independent characters will again be most useful. The higher the number of independent characters for which a divergence between both stocks will have been demonstrated, the clearer it will be that the genetic divergence between these stocks is high, and therefore that the process of differentiation or of speciation is advanced. However, even so, in many cases it will be impossible to conclude; only a field experimentation, putting in contact populations which have been separated by natural obstacles and which have diverged, would allow us to

Source : MNHN, Paris

know how they would behave then, and to decide if they are subspecies or species. No laboratory work will ever furnish an answer with certainty to this type of question, and such experiments are difficult to do with anurans, which are a little too big to be bred in demometers! The experiments of this kind realized by TWITTY (1961, 1964, 1966) on urodelans of the genus *Taricha* are, to the best of my knowledge, the only ones of this type to have been made in amphibians." (DUBOIS, 1977 b: 234, translated).

Similarly, the adoption of the genus concept here advocated implies the acknowledgement of a hierarchy in the use of the criteria presented above.

First, the fact that two species A and B are liable to produce viable adult hybrids is an absolute and definitive proof that both species possess very close functional genetic characteristics and must therefore be grouped together in a same genus (nonarbitrary criterion for *inclusion*). Given the complexity of Eucaryote genome, one may without hesitation exclude as completely impossible that such a genetic similarity could be obtained by convergence between two species of two phylogenetically distinct groups, and this criterion of hybridizability can therefore be also considered as a criterion of homophyly. But to entirely satisfy this criterion, the species A and B must belong to the same genus as their most recent common ancestor, which leads to grouping in this genus all the other species which, by other criteria (homophyly, morphological and ecological resemblance, etc.) were previously classed in the same genus as A and in the same genus as B.

In the absence of successful hybridization, this criterion cannot be used in a negative way. It will then be useful to compare the holomorph of the studied species, to ascertain whether discontinuities exist or not within the group in question. The presence of such marked holomorphological discontinuities, whatever their "size", provided they correspond to characters for which the supposed genetic determinism is complex and irreversible in the strict sense of the term, is a good argument for considering that several genera do exist (nonarbitrary criterion for *exclusion*). The groups which remain must finally be submitted to a cladistic analysis. If this analysis demonstrates the existence of phenomena of parallelism or of convergence, the existing polyphyletic groups in their turn must be broken up (nonarbitrary criterion for *exclusion*), to leave only homophyletic (i.e. holophyletic or paraphyletic) groups.

The criteria of morphological and ecological resemblance and of homophyly must always be used with caution for *inclusion*, because real morphological or ecological differences, as well as real convergences, may always escape analysis when the available information is insufficient (see e.g. in amphibians: MAXSON & WILSON, 1974; MAXSON, 1977; FOUQUETTE & DELAHOUSSAYE, 1977). The criteria of inclusion, except that of hybridizability, are less reliable in general than those of exclusion and here the experience that a systematist has of the group he studies takes all its importance.

Defined by this set of criteria, genera may be of very variable "sizes", some being monotypic while others containing very numerous species. It is therefore very useful to recognize taxinomic subunits below the genus. We shall examine them in more detail below, but a few words may be said here already.

The recognition of taxinomic subunits within the genus is mainly based on the type of divergences which exist between the different natural groups which phenetic analysis allows one to recognize. When these groups show between them appreciable ecological differences, without for all that being separated by discontinuities, they should be given the status of subgenera, while groups which do not show between them a marked ecological differentiation will be considered as species groups (and possibly, more finely, as species complexes, synkleptons, superspecies or ultraspecies). The subgenus category may also be used in some cases to conserve at least provisionally old well-known generic names when the older genera have been merged to satisfy the above criteria.

Source : MNHN, Paris

Conclusion

In his interesting work on cladism, Dupuis (1979: 52, translation mine) writes:

> " As a matter of fact, it is obvious that the current dispute of so many classical ideas in biology cannot be reduced to a simple affair of opinion and could never have been the fact of *taxinomists alone*, be them hennigians or others. It results, before everything, from the considerable contemporaneous progresses of experimental biology, of paleogeography, of paleontology. For this reason, I am persuaded that the convincing light in phylogenetic taxinomy will come from new *experimental facts*. Not long ago, to speak of experimentation concerning phylogeny might have been regarded as impossible. Today, immunotaxinomy, enzymotaxinomy, molecular hybridization, genes-structures relationships, ontogenetic regulations and epigenetic amplification have become experimentally accessible (it is roughly the ' experimental systematics ' of Crowson, 1970: 296). More numerous data in these fields will further modify our views of evolution. There is only to await the taxinomic constructions which they will impose on us. "

Although this author fails to mention interspecific hybridization among modern and interesting methods, the hybridizability criterion here advocated to recognize genera is typically a criterion of this " experimental systematics " which belongs according to Crowson (1970: 292) to the " future of systematics ". Obviously the application of criteria of this type will not be possible without appreciably modifying existing classifications. Let us hope that, despite this difficulty, the new criterion will be taken into consideration by taxinomists, and that it will escape the pessimistic prediction of Sibley & Ahlquist (1982: 14):

> " it may take a generation or two of systematists to win acceptance. "

Source : MNHN, Paris

GENETIC REVOLUTION AND GENIATION: THE GENUS AS AN EVOLUTIONARY UNIT

PHYLOGENY AND ONTOGENY

Biology is not a unified science as yet. There runs through it the fundamental divorce between what JACOB (1970: 14-15) calls the " integrist or evolutionary " attitude and the " tomist or reductionnist " attitude, which has played a great rôle, not only in the recent history of biology, but also in that of modern society (see for example COMMONER, 1969, in particular chapter III). Today's reality is that the second attitude is the prevailing one, and biology suffers from a radical division into varied " disciplines ", which are often completely separated from each other, or nearly so, and which use different concepts, so that the " specialists " can hardly share their experiences, their knowledge and their problematics. As a matter of fact, the differentiation into a certain number of disciplines was historically necessary to let the " science of life " blossom forth: one had to clarify the concepts, to refine the methods for the study and understanding of biological reality at its various levels of integration (molecule, cell, tissue, organ, individual, population, ecosystem). However, for a great many " specialists ", those " disciplines ", which had been artificially set up in order to render the study of extremely complex phenomena easier, or even simply possible, have finally become " sciences " as such. Nothing can be more dangerous than this attitude for the future of biology. Fortunately, a salutary reaction against it is now developing, and some biologists try to restore a comprehensive, synthetic approach to biology that takes into account all the specific attainments contributed by each of these disciplines: works such as *The Growth of Biological Thought* by MAYR (1982 a) or the *Traité du Vivant* by RUFFIÉ (1982), testify to the reality of this movement. Such attempts at synthesis, even though they cannot but remain incomplete and imperfect for the time being, can only be carried out within the framework of an evolutionary conception of biological facts, and it is only in such a perspective that the unity of biology may eventually be reestablished.

Although the " synthetic theory of evolution " has been discussed for a long time, the science of evolution itself has long remained a discipline separated from the other disciplines of biology, and the synthesis is not complete yet. There still remains today a wide gap between the approach of the study of evolution through population genetics on one hand, and the study of macroevolutionary phenomena which refers in particular to the recent notions concerning the genes of regulation on the order hand: this gap clearly shows for instance in the complete absence of any link between the two parts of the book *Evolution* published by Hermann about ten years ago (PETIT, 1976; ZUCKERKANDL, 1976 b; see DUBOIS, 1982 b: 372-373). The synthesis in this field has only just started, with works such as *Ontogeny and Phylogeny* by GOULD (1977), *Macroevolution* by STANLEY (1979), or *Embryos, Genes and Evolution* by RAFF & KAUFMAN (1983). The latter authors offer an interesting historical account that makes it possible to understand how the divorce between genetics and embryology came about at the beginning of the

Source : MNHN, Paris

twentieth century. The two disciplines are now becoming reconciled, in particular around the concept of genetic and developmental regulation, thus opening the way to a new field of research, viz. the genetics of development, which is of utmost interest for all biologists and especially for those who are trying to understand the modalities of evolution. As for STANLEY (1979), he proposes a brief historical account of the divorce that long separated paleontology from the study of the mechanisms of evolution. It is interesting to note that in both cases a large rôle was played by the " setting-off effect " of GOLDSCHMIDT's (1940) theories on the part acted in evolution by " hopeful monsters ": due to the blatantly erroneous nature of the genetic model proposed by this author, the " modern synthesis " of the theory of evolution has rejected not only that model, but also the indeniable evolutionary reality that had inspired it, namely the fact that evolution proceeds at least partly by sudden phenomena, what SIMPSON (1944, 1953) has named quantum evolution; in spite of some " prophetical " articles (among which, that of MAYR, 1954, in particular), it is only recently that the importance of this type of evolution, and above all the fact that it is closely related to the phenomena of speciation, have really been perceived.

It is surprising that, apart from a handful of isolated searchers, so many biologists should have been interested in morphology and its evolution within groups of animals without considering the processes of morphogenesis. Now, the adult forms of living beings that systematists compare between one another no doubt are the products of evolutionary processes (phylogenesis), but they are also the results of processes of development (ontogenesis). They can therefore not be compared with each others as objects, or " completed products ", can, without their growth being taken into account.

It is now clear that the evolution of the morphology of adults can be grasped only through the evolution of morphogenetic processes. The recent works on the biology of development (see e.g. RAFF & KAUFMAN, 1983) have revealed a certain number of fundamental processes the understanding of which calls for the notions — that are sometimes old but that one is only beginning to perceive clearly — of genetic regulation, canalization, induction, molecular and cellular interactions, pleiotropy, epistasy, etc. The ontogenesis of an individual now appears like a chain of interdependent processes influencing each other and following each other in series, etc. Any disruption in one of those processes (e.g. any change in a growth rate) may have great consequences as to the morphology of the adult, provided it remains compatible with the life of the animal. The morphological changes will be all the more important as the disrupting action has taken place at an earlier stage of development, as the whole chain of interactions, inductions, etc., posterior to that stage will be modified in consequence. It is therefore easy to understand why simple genetic alterations, bearing upon few genes or even a single regulatory gene, may give birth to a new adult morphology:

> " Macroevolutionary changes in development need not be extreme. We propose that in fact the initial steps for rapid, and ultimately, large evolutionary transitions require only that key regulatory genes be few in number and accessible to nonlethal genetic alterations in their functions. Initial, ' easy ' genetic changes, which may have significant effects on the organism and become established in a small population, are of necessity viable, and present open avenues for selection of successive genetic changes. Profound change may be rapid in this way without recourse to any instantaneous hopeful monsters. " (RAFF & KAUFMAN, 1983: 163).

Among the evolutionary mechanisms that are beginning now to be well-known and that enable such spectacular alterations at little cost (in terms of mutation), let us mention the genes having pleiotropic effects, the mutations that have consequences as to the rate of development or the sexual maturation (aneuchrony), and the homoeotic mutations (see e.g.: OUWENEEL, 1976; GOULD, 1977; DUBOIS, 1979 b, 1987 a; RAFF & KAUFMAN, 1983). The existence of genes having pleiotropic effects, for instance, has been known for a long time, but that has not prevented a great number of theoreticians of evolution from using the " one gene, one character " postulate. Today, two types of pleiotropic effects are recognized, viz. direct pleiotropy and relational

Source : MNHN, Paris

pleiotropy, the study of which is rich in information (see e.g. RAFF & KAUFMAN, 1983).

Another relatively recent idea, at least for neo-Darwinian evolutionists, which had already been expressed in the form it could take at the time by authors such as GOLDSCHMIDT (1940), is the very simple one that the ontogenesis of an individual, being a complex, integrated process with numerous interactions, obeys a certain number of constraints, and that not all modifications are possible, the development being for the great part "canalized" (see e.g.: ALBERCH, 1980, 1982; WAKE, 1982 a, 1982 b; WAKE, ROTH & WAKE, 1983). Similar ideas had, it is true, been mentioned incidently by the most "synthetic" theoreticians of evolution, yet no real discussion had been devoted to them, as is shown for instance in the following quote:

> "The students of development have various terms for these regulatory powers, such as *buffering*, *canalization*, and *developmental homeostasis*. These terms apply to models that help us to visualize the action of genes in the developmental process, but they should not blind us to our basic ignorance of the exact mechanisms by which the universally observed regulation during development is achieved. (For further details on the physiology of differentiation of tissues and organs in relation to gene action, refer to books on epigenetics.)" (MAYR, 1970: 168).

Recently, MAYR (1975, 1982 b) has stressed the importance of these notions, and that of concepts such as the "unity" or "cohesion" of the genotype. They shed a new light upon the phenomena of macroevolution, which had so far eluded scientific interpretation to a large extent and given room to numerous speculations.

In the light of the recent works on the biology of development, RAFF & KAUFMAN (1983) have shown how biological evolution could only be possible in some directions, because of the constraints imposed by the mechanisms of ontogenesis:

> "If the notion of developmental constraints limiting evolutionary directions has any meaning, it is in the sense that modifications of already existing developmental processes provide the most readily available route for evolutionary change. Once a modification becomes established, it in turn makes acceptance of changes in certain directions more feasible than others. But if existing developmental patterns constrain, they also provide opportunities for rapid evolutionary departures when selection pressures on morphology change because of their dissociability and apparently simple genetic controls." (RAFF & KAUFMAN, 1983: 355).

Besides, RAFF & KAUFMAN (1983) insist upon the fact that the regulatory genes which play an important rôle in the control of the morphogenesis are probably in small number by comparison to the structural genes that come into action during it :

> "In both the fly *Drosophila* and the sea urchin *Strongylocentrotus*, a relatively large proportion of the genes expressed at some time during the life cycle are expressed in a specific manner during ontogeny. The crucial question of how many of these genes control morphogenesis is simply unanswerable at present. The overall proportion of genes concerned with morphogenesis may be great, but paradoxically the number of genes that actually regulate morphogenesis may not be. Many structural genes required for morphological ontogeny provide essential products without which particular morphological entities could not be assembled. Yet these genes provide little in the way of regulatory information: They are instead regulated in their action. Genes of this type should not be thought trivial, however, because the products of some of them, as for exemple, tubulins, actins, or cell surface proteins, provide the actual machinery for cell shape-change and cell movements directly underlying morphogenesis. Much of the control exerted by regulatory genes, those genetic gray eminences, must be devoted to orchestrating the expression of ontogeny-specific structural genes. If regulatory genes were very large in number, interactions between

Source : MNHN, Paris

> them would be so complex as to render viable evolutionary changes nearly impossible." (RAFF & KAUFMAN, 1983: 299).
>
> "Ontogeny involves the activity of many genes expressed in a whole set of very stable processes In *Drosophila* about one-third of the total number of detectable genes are expressed in a developmentally specific manner, and are needed for successful completion of specific developmental stages. Nevertheless, the number of switches is small, and changes in switch functions may have correspondingly great effects in morphogenesis. It is important to note, however, that evolution is not a single-step affair. The chief significance of alterations in genes with regulatory functions may be to produce changes in ontogeny that provide the raw material for further changes in a new direction. Further change and consolidation of the novel direction occur through mutational events in genes modifying the principal regulatory gene. Canalization and integration can be retained in the midst of evolutionary transitions in morphogenesis." (RAFF & KAUFMAN, 1983: 344).

RAFF & KAUFMAN's (1983) work is enthralling and will no doubt prove very useful to all the biologists who want to know more about the present state of our knowledge in the genetic determinism of morphogenesis, particularly in order to better understand the relations between the latter and evolution. However, although it begins with a criticism of the partitioning of biology which had long separated genetics from embryology, this book is not yet the synthesis that one may be expecting and that the title of its last chapter seems to be heralding: "Regulatory hierarchies and evolution: a synthesis". The reason for it is simple: just as GOLDSCHMIDT (1940), to whom they dedicate their work, RAFF & KAUFMAN (1983) do not understand that biological evolution is not an evolution from organism to organism, from individual to individual, but that it consists on the contrary in a process that has to do with *populations*. In this respect, the lack of any reference to MAYR's works in their bibliography, as well as the lack of any discussion of the fundamental phenomena of populations genetics, of the genetic revolution, or even of speciation in general, testify to a serious shortcoming. As MAYR (1942, 1963, 1970, 1982 b, 1982 c), RENSCH (1959) or STANLEY (1979), for example, have emphasized, no theory of evolution can evade the central problem of speciation:

> "(...) I feel that it is the very process of creating so many species which leads to evolutionary progress. Species, in the sense of evolution, are quite comparable to mutations. They also are a necessity for evolutionary progress, even though only one out of many mutations leads to a significant improvement of the genotype. Since each coadapted gene complex has different properties and since these properties are, so to speak, not predictable, it requires the creation of a large number of such gene complexes before one is achieved that will lead to real evolutionary advance. Seen in this light, it appears then that a prodigious multiplication of species is a prerequisite for evolutionary progress. (...)
>
> The evolutionary significance of species is now quite clear. Although the evolutionist may speak of broad phenomena, such as trends, adpatations, specializations, and regressions, they are really not separable from the progression of entities that display these trends, the species. The species are the real units of evolution, as the temporary incarnation of harmonious, well-integrated gene complexes. And speciation, the production of new gene complexes capable of ecological shifts, is the method by which evolution advances. Without speciation there would be no diversification of the organic world, no adaptive radiation, and very little evolutionary progress. The species, then, is the keystone of evolution." (MAYR, 1963: 621).

RAFF & KAUFMAN's (1983) "synthesis" remains therefore very incomplete. They show us convincingly enough that great alterations in the morphology may be produced by only a few mutations affecting the regulatory genes, but they are not concerned with the mechanisms that may be responsible for the appearance and fixation of such mutations in natural populations,

Source : MNHN, Paris

whereas it is only when such mechanisms are known that we shall really be able to begin to understand the phenomena of speciation and of macroevolution.

I think it is only through a synthesis of the modern data related to the genetics of development and to the study of speciation (with the help of the concepts and techniques of populations genetics, among others), that apprehending evolutionary phenomena will prove possible, as MAYR (1970, 1982 b) has already stressed it:

> " Much that is now explained as ' epistatic interactions between different loci ' might well be due to the activities of regulatory genes. (...)
> The day will come when much of population genetics will have to be rewritten in terms of the interaction between regulator and structural genes. This will be one more nail in the coffin of beanbag genetics. It will lead to a strong reinforcement of the concept that the genotype of the individual is a whole and that the genes of a gene pool form a unit. " (MAYR, 1970: 183).
> " We now know that the genotype, even though all of it is composed of DNA, consists of highly heterogeneous classes of DNA, each of which is likely to have a somewhat or altogether different function. Those of us who for a long time have been on the road toward the explanation of speciation and evolution and who thought that we were nearing the goal now feel suddenly like the player in a parlor game who is told to go back to position zero. Indeed as far as our understanding of the genetics of speciation is concerned we are almost at position zero. " (MAYR, 1982 b: 1124).

Another recent attempt at a synthesis is that by STANLEY (1979). Contrary to RAFF & KAUFMAN (1983), this author grants the study of speciation all the importance it deserves, and he relates it to the notion of genetic regulation, but other evolutionary phenomena are underrated this time, namely those of selection and adaptation on the scale of populations. STANLEY would probably agree with MAYR (1978: 478), when the latter remarks with surprise

> " how little population genetics has contributed to our understanding of speciation ".

Yet, whatever its importance, speciation is not *everything* in evolution, and the lack of any concern for the results of populations genetics in STANLEY's (1979) work restricts the interest of this book within the limits of a study of macroevolutionary phenomena (as its title indicates).

The overall synthesis of what we know about all evolutionary phenomena remains to be written, and I cannot share STEBBINS & AYALA's (1981), optimism in this respect, who consider that such a synthesis would only call for a small transformation of the " modern synthesis ", or that of MAYR (1982 b) who does not deem a transformation at all necessary — see GOULD & LEWONTIN (1979), GOULD (1980), WAKE, ROTH & WAKE (1983), etc.

The preceding remarks will enable us to consider the problem of the modalities of appearance of new genera in evolution: indeed it is typically a field in which the various types of phenomena above mentioned meet (at the level of the genotype and of development; at the level of populations).

PHYLETIC GRADUALISM AND QUANTUM EVOLUTION: ARE GENERA DISCONTINUOUS?

As far as the genus, first of the higher categories, is concerned, one may ask oneself, in a simple and almost testable way, the fundamental question of the study of macroevolution: do evolutionary innovations, i.e. new types of morphologies, appear in a strictly *progressive* way,

Source : MNHN, Paris

without disruption, without interruption, as some of the theoreticians of the synthetic theory of evolution claim (e.g.: THALER, 1982; CHARLESWORTH, LANDE & SLATKIN, 1982; BARTON & CHARLESWORTH, 1984), or does their rise need some sort of disruption, a sudden evolution, of the *quantum* type, such as SIMPSON (1944, 1953) or STANLEY (1979) define it? According to the second hypothesis, two possibilities still remain: either quantum evolution requires passage through a " hopeful monster " as defined by GOLDSCHMIDT (1940), as the authors of the theory of *punctuated equilibria* seem to think; or this evolution occurs on the occasion of a *genetic revolution*, as MAYR (1954) defines it, or of other similar mechanisms.

In a very interesting work, LEMEN & FREEMAN (1984) have recently regarded this problem in an original manner, that is by studying, in three families of microchiropterans, the way species were distributed in a given hyper-space defined by a multivariate analysis of their morphology, in which the " size " and " shape " components of the latter were dissociated by means of allometrical curves of growth (the successive morphologies along the same curve were interpreted as being the same " biological shape ", though differing between each other only by the " size " factor, whereas the changes perpendicular to the curve correspond to a change in " shape "). They compared these data gathered from three real groups of animals to the data obtained through simulation from three evolutionary models based upon different postulates: (1) a " uni-modal " model, compatible with a gradual evolution, in which the morphological changes of a character through time have a normal distribution; (2) a " decoupled " model, in which there exist two different types of evolutionary events causing the morphological alteration, some being linked to size, and the others not (" decoupled "); (3) lastly, a "saltational " model, in which there also exist two types of evolutionary events, some linked to size, and the others of the saltational type (alterations of a great amplitude, but in which size and shape remain correlated).

Regarding the three families of bats studied, LEMEN & FREEMAN (1984) have shown that the genera such as systematists acknowledge them today correspond to groups of species of similar " shapes " but of variable " sizes "; conversely, a significant alteration in " shape " may be observed from one genus to another. Comparing those results to those obtained with the three models described above, LEMEN & FREEMAN (1984) noticed that only one of these models, namely the " decoupled " one, yielded similar results, while the other two models did not produce such groups of species " variable in size but homogeneous in shape ". LEMEN & FREEMAN's (1984) conclusion is that these results are consistent with the hypothesis according to which evolution would proceed in two successive stages; first, diversification in " size " within a group of species of similar " shapes "; then, dissociation of characters previously correlated, and appearance of a new group of species with a different " shape ". The authors deduce from this that size and shape do not diversify in the same way, and that the two processes should be considered as different evolutionary events: the interaction between these two types of evolution would produce the groups of species one observes, that are homogeneous as far as " shape " is concerned, and greatly heterogeneous as far as " size " is concerned; and such groups are those that are generally considered as genera by systematists. They can be holophyletic or paraphyletic (that is to say that groups defined thus can rarely be formed by convergence of several independent lineages). The importance of the " distance " that separates such groups may vary, and it depends upon that of the "decoupled jumps " that enable the passage of one " shape group " to another, or upon the nature of the adaptive zones: hence, there does not always exist a *gap* between these groups, but there always exists a *discontinuity*. Finally, the respective rates of " correlated " or "decoupled " events in the evolution of a given group will determine the number of species in each genus, and the diversity in shapes of that group.

As a conclusion to their work, LEMEN & FREEMAN (1984: 1236-1237) write:

> " We can speculate that the evolutionary mechanism that makes shape-conservative genera may work at higher taxonomic levels as well. This idea leaves us to wonder to what extent the typological concept of discrete hierarchical categories in systematics might have originally hinged on the

Source : MNHN, Paris

shape groups produced by the interaction of two different processes, the evolution of size and the evolution of shape. "

LEMEN & FREEMAN's (1984) paper does not answer some of the questions that its reading may raise (DUBOIS, 1988):

(1) What definition of the genus do these authors use, or advocate? They do not make a clear choice between today's various theories of zoological classification:

" We take no stand on how genera are actually formed, or on how genera should be formed " (LEMEN & FREEMAN, 1984: 1220).

As a matter of fact, they seem to opt for an empirist conception of classification, since they consider

" the actual formation of genera difficult and perhaps a matter of art in science " (LEMEN & FREEMAN, 1984: 1236).

(2) What do they mean by expressions such as " real genera " or " the real world ", which frequently appear in their text? Do they mean genera that are " real " in the taxinomic practice (by opposition to an " ideal " definition or conception of the genus, or to the artificial groups that may produce the computer simulations such as the ones they use in their work), or genera that are " real " in nature, and exist independently from the systematists' idea of them? A close reading of their article reveals that the expression " real genera " takes either of these two meanings alternatively in various parts of the text. It is true that the two meanings do not necessarily exclude one another: it is indeed quite possible to claim, as I am precisely doing in this paper, that there exist in nature, as a consequence of biological evolution, " real entities ", real groups of species to which the category of genus can be applied; the systematists' task would then be to recognize or identify such entities in nature rather than to try to construct artificial groups. It seems that such an idea is in the back of LEMEN & FREEMAN's (1984) minds, for instance when they write:

" It is the interaction of the evolution of size and shape that produces the shape-conservative groups that can vary greatly in size. " (LEMEN & FREEMAN, 1984: 1236).

However, if such an hypothesis is made, it should be clearly stated. Moreover it entails other consequences: for example, if the genera exist, and must be recognized, in nature, it cannot simply be a matter of " art ", but *scientific* rules must be proposed in order to reach such a goal, contrarily to what LEMEN & FREEMAN (1984) write.

(3) LEMEN & FREEMAN (1984) do not question the nature of the genetic phenomena likely to be responsible for the two fundamentally different evolutionary processes that they think account for the rise of the groups, homogeneous in " shape " and variable in " size ", that they have found. What can these mechanisms be? That is what I am now going to try to deal with.

However, let me first note that the discontinuity between genera, clearly expounded in LEMEN & FREEMAN's (1984) work, has been known by systematists for a long time. It can be shown by various methods of study of morphology, but also, in quite a different way, by the study of hybridization: as we have already seen above, the study of the lists of species likely to generate viable hybrids makes it possible to acknowledge the existence of closed groups, of varied sizes, not that of a continuum of species hybridizable step by step. Moreover, these groups of potentially hybridizable species happen to have long been recognized as systematic units, although the rank given to those taxa may vary from one group to another (genus, family, etc.): my proposition to use the criterion of hybridizability to define genera boils down to choosing a level of standardization and making the two types of discontinuities

Source : MNHN, Paris

(according to morphology and to hybridizability) coincide. The fact that the two criteria can coincide rather easily shows that the discontinuities between genera are mainly due to the particular conditions in which the genera appear, rather than to the extinctions of so-called intermediate species which some authors refer to, maybe for fear they should have to believe in " hopeful monsters " instead, in order to be able to account for the phenomena of " saltation " in evolution. It is therefore interesting now to consider the processes involved in the birth of genera.

Transilience, genetic revolution and geniation

Geniation

In 1981, I proposed the use of the new term *geniation* (from the Latin *genus*) to describe the " appearance or birth of a new genus " (Dubois, 1981 c: 508). The use of such a term implies that one admits that there are indeed entities in nature that one can call by the name of genus, and that the entities in question are not only creations of the human mind. If one admits that these entities do exist, it is legitimate to devote attention to the mechanisms responsible for their birth or appearance. However, the term "geniation " in itself does not imply any mechanism *a priori*: one can envisage a *gradual geniation*, i.e. a progressive one, and a *quantic geniation*, i.e. a rapid and sudden one.

If we are to believe Lemen & Freeman (1984), genera appear in nature as a result of "decoupled events ", during which the " size " and " shape " factors of the morphology of the organisms happen to be decoupled or separated for some time. As we have seen, it is therefore a question of discontinuous events, of the quantic type and not of the gradual one.

Lemen & Freeman (1984: 1221) call the model that describes such events by the name of " decoupled/adaptive zone model ". They thus refer to the concept of *adaptive zone*, as it was formulated by Simpson (1944, 1953). Each genus may be considered as a group of species occupying a given adaptive zone. The basic idea upon which this conception is grounded is the following one: adaptive zones are *discontinuous*, and the passage from one to another requires important genetic alterations, that are *irreversible at little cost* (Dubois, 1975, 1976, 1981 c, 1982 a). The passage into a new adaptive zone requires the crossing of a *gap of adaptive disequilibrium* which separates it from the previous one (Simpson, 1944, 1953). The question is to know how this gap can be crossed.

Concerning this, Simpson's hypotheses remain vague and quite debatable: he proposed the formula of *quantum evolution* to describe this type of events, but the mechanism suggested (fragmentation of a large population into small, isolated populations, then passage of the latter through a " non-adapted " phase before "accosting " in a new adaptive zone) is not very likely (Pasteur, 1982: 512). Moreover, Simpson did not propose any genetic model to account for this quantum evolution (Dubois, 1982 b: 398).

Mayr's model of genetic revolution

The first coherent model proposed in this respect is that of the *genetic revolution* of Mayr (1954, 1963, 1970, 1975). It is a particular model of speciation, which belongs to the more general category of speciation called " peripatric speciation " by Mayr (1982 b, 1982 c), in which the emphasis is laid upon: (1) the isolation, in adverse environmental conditions, of one or

Source : MNHN, Paris

several founder individuals from the initial population (large, panmictic and with an important genetic polymorphism); (2) the reorganization of the genotype on new bases; (3) the passage into a new adaptive zone. This model comes as a complement to SIMPSON's quantum evolution (1944, 1953), with which it is quite compatible (DUBOIS, 1982 b), and PASTEUR (1982: 512) has suggested combining the two theories under the general name of " SIMPSON-MAYR model of transspecific evolution ". The concept of genetic revolution would thus make it possible to account for the cases of " sudden " appearance of completely new types of organization within homogeneous groups which have drawn the evolutionists' attention for quite a while.

The genetic revolution would not so much consist in the appearance of new mutations as in a re-organization after a new mode, of the genes already present in the initial stock. In his work of 1954, MAYR already insisted upon the fact that the most important aspect of this event would be the great rise in the degree of homozygosity in the small isolated founder population. In this small population, the homozygosity would be maintained, and even increased through generations. It would affect the selective value of many genes, as well as the overall internal equilibrium of the genotype. Under the effect of the heavy natural selection that would affect this population, the genotype would be profoundly altered, before reaching a new stade of equilibrium. The population could thus go from one " adaptive peak " to another, to take up WRIGHT's (1932) image. MAYR (1954: 169-170) does not write that all the genes would be directly modified, but that they would at least be " affected " in their " genetic environment " and their selective value:

> " We come thus to the important conclusion that the *mere change of the genetic environment may change the selective value of a gene very considerably*. Isolating a few individuals (the ' founders ') from a variable population which is situated in the midst of the stream of genes which flows ceaselessly through every widespread species will produce a sudden change of the genetic environment of most loci. This change, in fact, is the most drastic genetic change (except for polyploidy and hybridization) which may occur in a natural population, since it may affect all loci at once. Indeed, it may have the character of a veritable ' genetic revolution '. Furthermore, this ' genetic revolution ', released by the isolation of the founder population, may well have the character of a chain reaction. Changes in any locus will in turn affect the selective values at many other loci, until finally the system has reached a new state of equilibrium. "

One understands therefore why various authors ascribed to MAYR the idea that most genes would be altered, an idea that will not hold up under a close scrutiny, and that MAYR himself (1982 b: 1124) claims he never held:

> " I did not claim in the least that every founder population experiences a genetic revolution. Neither did I claim that all or even most genes were genetically affected. All I claimed was that by changing their genetic milieu the phenotypic expression and hence the selective value of many genes would be affected. "

The process described above, which would occur in some isolated populations but not in all, might lead to the appearance of morphological innovations and enable passage into a new adaptive zone.

MAYR (1982 a, 1982 b, 1982 c) has recently proposed a slightly modified phrasing of his theory, which takes into account recent developments of genetics and of the study of speciation. The most important characteristic of what he now calls peripatric speciation is the reorganization of the genotype on new bases, without, however, most loci being modified:

> " the gene pool of a small either founder or relict population is rapidly, and more or less drastically, reorganized, resulting in the quick acquisition of isolating mechanisms and usually also in drastic morphological modifications and ecological shifts. It involves populations that pass through a bottleneck in population size. " (MAYR, 1982 c: 4).

Source : MNHN, Paris

MAYR's hypotheses on genetic revolution have given rise to numerous criticisms, some of which are important (LEWONTIN, 1965; LANDE, 1980; CARSON & TEMPLETON, 1984), the main one being probably the fact that this model is based upon conditions that are mutually contradictory in populations genetics:

> " Genetic revolution requires a significant increase in homozygosity relative to the ancestral condition. By emphasizing that the founders come primarily from peripheral demes, however, MAYR makes it more difficult to satisfy this requirement in the many species in which peripheral demes are already characterized by inbreeding and increased homozygosity. More damaging is the fact that a population's ability to respond to intense selection is directly proportional to the amount of genetic variation it has. Yet the genetic revolution model demands a rapid and effective response to selection precisely when genetic variation is at a minimum — conditions that make a rapid and effective response impossible. Thus, MAYR's genetic revolution model is based upon mutually contradictory population-genetic conditions. " (CARSON & TEMPLETON, 1984: 119).

OTHER MODELS OF GENETIC REVOLUTION

Other models of speciation by founder-effect were proposed after MAYR's (1954). Thus CARSON (1975, 1982) proposed the " founder-flush speciation theory " (POWELL, 1978), recently rediscussed by CARSON & TEMPLETON (1984), which, as its name indicates, calls on a founder-effect followed by a demographical explosion.

In a fundamental paper, CARSON (1975) has suggested that every diploid species has two distinct systems of genetic variability. The " open " system consists in all the genes which are frequently polymorphic and which can recombine freely without this having important consequences on the viability: he mentions as examples of such genes those that intervene in enzymatic polymorphism, in clinal and subspecific variability. These genes may be introgressed from one species into the other in the case of species that can occasionally hybridize in nature (SENE & CARSON, 1977). On the contrary, the " closed " system consists of " internally balanced gene blocks " forming coadapted complexes. Such *supergenes* (DARLINGTON & MATHER, 1949: 46) can be preserved from dissociation by recombination for instance by the presence of inversions (see WASSERMAN, 1968). Their dissociation by crossing-over leads to an important reduction in viability in the normal conditions of natural selection. These blocks are stable within a species but different from one species to another. They cannot be introgressed by hybridization from one species to another (SENE & CARSON, 1977). Speciation therefore requires that the existing blocks be broken and new ones established.

Recent studies on the structure and the working of the genome of Eucaryotes have made it possible to state more precisely the nature of the supergenes which make up the " closed " genetic system such as CARSON (1975, 1982) conceives it. Here is how DEMARLY (1979) defines the concept of *linkat*:

> " The linkat is presented as:
>
> 1. A set of loci which aggregated in a same chromosomal sector during species differentiation. These clusters show strong epistasy and generally represent coadapted functions.
>
> 2. Each of the loci are constituted by a series (of) duplicated transcriptional units. Their expression has some flexibility caused either by hierarchical repression or derepression between slightly differentiated duplicates or by rearrangements of introns to exons after DNA transcription, which breaks the dogma ' one gene one polypeptide chain '.
>
> 3. On these chromosomal segments the allelic arrangements which

Source : MNHN, Paris

possess the highest adaptive value have been stabilized by genic and epigenic factors lowering the rate of recombination between them. Therefore they are inherited as a semistable block.

4. In some case it could be postulated that these arrangements contain inside them antimutator factors which give a longer perennity to the clusters.

Therefore linkats appear to be semi-stable functional units, the expression of which having some flexibility following environmental correlations and genetic background. This concept is included in a genetic system which minimizes genetic load. " (DEMARLY, 1979: 258).

In the " founder-flush " model of speciation, a founder population is isolated from an ancestral polymorphic and coadapted population. The genetic drift that follows the foundation event starts desorganizing the ancestral coadapted genetic complex. As the population settles into its new environment, it goes through a phase of demographic explosion, in which, due to the slackening of natural selection, the genetic variability of the ancestral population is not only preserved, but also increased by phenomena of recombination and of alteration of the pleiotropic equilibria. At the end of this phase of demographic explosion the population is therefore highly polymorphic. The environment becoming saturated the selective forces appear again, and they can entail a new phase of mass mortality, which can lead to the surviving of only one or a few individuals, in which the initial balanced and coadapted genetic systems may happen to have been modified and reorganized in a different way. Those atypical individuals, characterized by a new coadapted " closed " genetic system, can be at the origin of a new species.

The model of " genetic transilience " proposed by TEMPLETON (1979, 1980 a) and recently rediscussed by CARSON & TEMPLETON (1984) is close to the preceding one, in so far as it does not call on a sharp increase in the degree of homozygosity. However, in this model, the main factor of selection, instead of being external (high selection after the period of demographic explosion), is endogenous, viz. it is a modification at random, in a very limited population, of the frequencies of some rare " major alleles ", i.e. genes with important pleiotropic effects. The alteration of the initial frequencies of these alleles can end up in the fixation of some of them in the homozygous state. The resulting transformation of the genetic environment leads to a fundamental change in the selective value of the genotype, and the population enters a new phase of selection. If the founder population has a high genetic variability at numerous loci (and therefore a high heterozygosity), it may happen to react to this selection in rapidly shifting towards a new state of genetic equilibrium (a new coadapted genotype).

The validity of CARSON's (1975, 1982) and TEMPLETON's (1980 a) models is supported, not only by a theoretical study of them (CARSON & TEMPLETON, 1984), but also by laboratory works (POWELL, 1978; WALLACE, 1978; TEMPLETON, 1979; ARITA & KANESHIRO, 1979; AHEARN, 1980), as well as by the study of the speciation processes in certain groups of animals, the most spectacular of which in this respect being that of Hawaii drosophils (CARSON & KANESHIRO, 1976). In quite a different group, that of geckos, PASTEUR (1964, 1977, 1982) has also shown that some phenomena of speciation can obviously be explained by such founder-effects.

In their recent works, TEMPLETON (1980 a, 1980 b, 1981, 1982) and CARSON & TEMPLETON (1984) have not merely described the process of genetic revolution, but they have also endeavoured to incorporate theoretical concepts of populations genetics into the study of the process in question. They have thus shown that genetic revolution can only take place in some very precise conditions, not only ecological and geographical, but also genetic: in other words, only some species are a good " ground " for such an event. Therefore these authors do not claim in the least that all the events of speciation occur by genetic revolution, but only that *some* of those events do so. Moreover, they insist upon the fact that there exist several distinct types of genetic revolution:

" there is not one founder principle in speciation, but several " (TEMPLETON, 1980 a: 1030).

Source : MNHN, Paris

As for PASTEUR (1982), he gave a list of the properties (predispositions, preadaptation, other properties) of an ancestral species, or of some of its populations, that will render easier or possible the birth out of it of a daughter species by effect of founder and genetic revolution.

In this respect, it is interesting to note that one's agreement with the theory of genetic revolution (speciation by founder-effect) does not at all imply that one should automatically agree with the recent theory of punctuated equilibria (ELDREDGE & GOULD, 1972; GOULD & ELDREDGE, 1977; STANLEY, 1979; GOULD, 1982). First of all, results compatible with this model can be obtained by other models than that of speciation by founder-effect (CARSON & TEMPLETON, 1984). Secondly, it is not true that, as STANLEY (1979) or GOULD (1982) thought, the reference to a model of genetic revolution should imply that selection and adaptation in a given species (" phyletic gradualism ") do not play any evolutionary rôle. Indeed, the main rôle of genetic revolution is to free the species from the epistatic constraints of its coadapted " closed " system, but, once that done, a new coadapted " closed " system will still have to be built again, which cannot be an instantaneous phenomenon. From this point of view, there is agreement between authors who developed different models of genetic revolution, such as MAYR, CARSON and TEMPLETON:

> " The evolution of a new coadapted gene complex (the event actually associated with the development of a new species) generally occurs *after* the genetic revolution, and it occurs via the normal operation of selection, mutation, drift, and so on within a single breeding population. The inference that microevolutionary processes are unimportant in speciation because of genetic revolution is totally unfounded. " (CARSON & TEMPLETON, 1984: 126).
>
> " What is crucial is the fact that prior epistatic and regulatory systems are broken up during a genetic revolution in the founder population, making room for new ones. This greatly facilitates and speeds up the acquisition of new adaptations. These are, of course, not acquired by single steps, and selection for their improvement continues. It may even be accelerated by the establishment of descendant founder populations. It is unknown and presumably variable whether such an evolutionary shift requires a few, scores, hundreds, or thousands of generations, but it is certainly by several orders of magnitude faster than the traditional phyletic evolution described in the paleontological literature as requiring millions of years. Even so, evolution through changes in founder populations is not a process of saltation but one of gradual evolution. The most important departure in the new way of thinking is to treat it as a populational phenomenon. " (MAYR, 1982 a: 618).
>
> " One of the major effects of the disorganization described above is that it often may bring the relevant population close to extinction. Numbers become small; adaptations are impaired by stochastic effects. The mean fitness of the population is lowered as the various balanced genetic components of the gene pool are destabilized. If the population is to survive the threatened extinction, then, the generations that immediately follow the disorganization phase become crucial. Under these circumstances, a change in ambient environment is not a necessary prerequisite for genetic change. It is not a matter of the details of the genotype slavishly tracking the environment. What has happened is that the former genetic organizations of the gene pool, its old epistases and balances, are suddenly in disarray. Accordingly, selection begins to actively form new balances, using the remnant genetic elements segregating in the depauperate gene pool, which may continue to have a small effective size.
>
> The ensuing one hundred to one thousand generations are considered crucial in the building of the organization of the new gene pool, and the synthesis of the new adaptations. In fact, this stage in the life history of the species, in this reductionist view, is the most important one from the point of view of progressive, significant genetic change per unit time. It is during this time that the adaptations characteristic of the species as a whole are forged by mutation, selection, and recombination along with other corre-

Source : MNHN, Paris

> lated morphological, behavioral, and physiological novelties of the new species. Basically, it is a gradual, anagenetic intrapopulational process; there is nothing saltational, rectangular, punctuated, concerted, or instantaneous about it. Macromutations and mutations profoundly affecting development are not required. As the gene pool expands in size and gradually equilibrates, the rate of genetic change is gradually reduced. In most diploid organisms, what has been achieved is considered to be a new complex dynamic balance, not a new fixed homozygous state. The biggest change may well be a change in internal genetic environment and interaction between the many component genes." (CARSON, 1982: 423-424).

For the paleontologist, some events may seem to have been "instantaneous", while they took place over a span of many generations: neontologists and paleontologists work on different "scales", which accounts for the basic difference in their appreciation of the more or less "gradual" nature of evolutionary phenomena (see e.g. MAYR, 1982 b).

Besides, TEMPLETON (1980 a) has emphasized that numerous fossil groups, the history of which had been interpreted as supporting the theory of punctuated equilibria, probably did not meet the requirements enabling speciation by founder-effect:

> "Consequently, founder-induced speciation models do not provide either a general theory of macroevolution or a general interpretation framework for the fossil data." (CARSON & TEMPLETON, 1984: 126).

The theory of punctuated equilibria suffers also from other difficulties or incoherencies, that MAYR (1982 b), for instance, has analysed. There exist several versions of this theory. The two extreme ones are, on one hand, a moderate, Mayrian or Simpso-Mayrian one, which acknowledges that genetic revolution is a gradual and populational, albeit very rapid, phenomenon, and on the other hand a drastic, or Goldschmidtian one, which refers back to notions such as "systemic mutations" or "hopeful monsters". The latter overlooks the populational aspect of evolutionary phenomena, and is only an inacceptable simplification of the observed facts.

GENETIC REVOLUTION AND CHROMOSOMAL REARRANGEMENTS

It is tempting to try to "visualize" genetic revolution, in particular at the chromosomal level. Thus, WILSON, SARICH & MAXSON (1974) have suggested that a genetic revolution could be caused by a rearrangement of the position of the genes on the chromosomes; WILSON *et al.*'s (1975) data go in the same direction. According to these authors, such chromosomal rearrangements would be particularly frequent and rapid in the groups in which the effective size (WRIGHT, 1931) of the reproductive populations is low (WILSON *et al.*, 1975, 1977; BUSH *et al.*, 1977), such as the founder populations in the models above mentioned. The chromosomal rearrangements in question would entail alterations in the systems of genetic regulation, without a modification of the structural genes, but with changes in the rates of the different types of molecules that regulate genetic activity, and, consequently, in the quantitative relations between the activities of various genes, crossings of thresholds (ZUCKERKANDL, 1979, 1980). These changes in the systems of genetic regulation could have far-reaching consequences as regards both morphology, and postzygotic isolation from the initial stock. If it is clear that all the cases of speciation, including those by genetic revolution, do not fit within the framework of this model, it is difficult, for the time being, to guess the proportion of cases of speciation that do fit in it. According to WHITE (1978: 324), more than 90 % of the cases of speciation would be accompanied by chromosomal rearrangements, but the nature of the implications of those rearrangements, particularly what has to do with the mechanisms of genetic revolution, is still very poorly known:

Source : MNHN, Paris

> " In fact, each chromosomal rearrangement — whether fusion or dissociation, translocation, inversion, gain or loss of heterochromatin — must be regarded as a unique event whose consequences will be almost impossible to predict in the present state of our knowledge. " (WHITE, 1978: 336).
>
> " It seems unlikely that the chromosomal rearrangements that lead to changes in chromosome number or in the number of chromosome arms would themselves directly produce regulatory genetic changes. " (WHITE, 1982: 88).
>
> " The introduction of the concept that changes in gene regulation may have greater evolutionary significance than changes in the genes themselves has had a major impact on evolutionary studies in the last decade. (...) By potentially altering the *cis*-acting regulatory circuitry, a chromosome rearrangement may affect gene regulation, and thus organismal phenotype. (...) There is, bowever, little hard evidence on the types of chromosomal rearrangements observable by standard cytogenetic techniques that supports this view. On the contrary, systematic studies of rodents have discovered numerous examples of cryptic chromosomal ' species ', many of which involve substantial reorganization of the karyotype. (...) In these cases, cytological rearrangements have had no discernible phenotypic effects ; those that do produce noticeable pathologies would be rapidly eliminated from natural populations. (...) Phenotypic changes clearly are not a general consequence of karyotypic change. " (PATTON & SHERWOOD, 1983: 149).
>
> " There is a reciprocal relationship between chromosome structure and gene function. The role of genes in determining the behavior, function, and even structure of chromosomes has been almost entirely neglected and is absent from discussions of the role of chromosome change in population divergence. The data available to date suggest that chromosome change may well be of secondary importance in processes of speciation and phyletic divergence. " (PATTON & SHERWOOD, 1983: 152).
>
> " Our own view is that genomic reorganization is crucial to morphological evolution. However, these changes are achieved by mechanisms more subtle than gross chromosomal rearrangement, and gross changes are not a necessary component of speciation and morphological change. " (RAFF & KAUFMAN, 1983: 82).

It is therefore probable that there does not exist a straightforward relation between chromosomal rearrangements and the evolution of the systems of genetic regulation which is itself associated with speciation and morphological evolution. This independence is stressed by the now well-known fact that speciation can occur without rearrangements, as for instance certain species of Hawaiian drosophils show (CARSON, CLAYTON & STALKER, 1967; CARSON & KANESHIRO, 1976; etc.).

GENETIC REVOLUTION AS A MODE OF SPECIATION AMONG OTHERS

Some general conclusions can be drawn from what has just been said.

First, it is certain that, in small, isolated populations, a fundamental reorganization of the genotype may occur under certain circumstances, which can lead to an alteration in the morphology, to the passage into a new ecological niche, and to the rise of a new species which may be the starting point for a new genus.

Several mechanisms have been proposed to try to explain how such a reorganization of the genotype can take place and, above all, how it can be fixed in the founder population. Some of these mechanisms are not very likely, others are more so, but the concrete data, based as much upon experimental facts as upon study of natural populations and species, have so far remained too scanty and lacking in details to make it possible to know which mechanisms really operate in nature, and what is the relative importance

Source : MNHN, Paris

of each of them at the global scale of evolution. However, it is quite probable that there does not exist only one mechanism likely to produce such a result, but several, which are not all known as yet (even as " models ").

It would be advisable in this respect not to repeat the mistake that had been made in the case of the general study of speciation, where controversies went on for years: these controversies were partly distorted because in particular they were based upon the erroneous hypothesis whereby all the cases of speciation had to obey similar mechanisms. Various recent works have on the contrary led to the conclusion that there certainly exist several well distinct types of speciation (see e.g.: SCUDDER, 1974; BUSH, 1975; CARSON, 1975, 1982; ENDLER, 1977; PASTEUR, 1977, 1982; WHITE, 1978; TEMPLETON, 1980 a, 1980 b, 1981, 1982; BARIGOZZI, 1982; ROSE & DOOLITTLE, 1983; CARSON & TEMPLETON, 1984; BARTON & CHARLESWORTH, 1984). These different modes of speciation are in particular related to the type of ecology of the ancestral species (type of environment, size and structure of the populations), with their genetic structure and with the geographical conditions (see e.g. the various chapters in BARIGOZZI, 1982):

> " Quite often it has been concluded that one aspect of evolutionary change is the most important one with respect to speciation, such as karyotypic evolution (...), or that certain levels of genetic divergence correspond to certain levels of taxonomic status. (...) However, the evidence has dashed all these hopes: Speciation can occur in the absence of, or is uncorrelated in some groups with, karyotypic change (...), significant DNA sequence divergence (...), significant isozyme differentiation (...), morphological change (...), and shifts in niche or habitat (...). These studies do not imply that these factors are never involved in speciation, simply that one factor is not critical or necessary for all modes of speciation. Because of the failure of individual elements to identify a universal marker of speciation, some workers have investigated joint patterns of two or more of these differences and their relation to speciation. For example, in some vertebrates, karyotypic and morphological evolution are positively correlated with each other and with speciation rates, whereas protein evolution is uncorrelated with all the others (...). However, other studies do not support this pattern (...). Thus, there is also no universal joint pattern relative to speciation. However, predictable patterns and differences do emerge for particular groups of organisms (...), and population-genetic considerations are apparently important determinants of these patterns (...). " (TEMPLETON, 1981: 24).

Despite this diversity, it seems possible to classify the different modes of speciation into two main categories. The speciations that belong to the first category are slow phenomena in which genetic differences are gradually accumulated between separated populations; when the latter are brought in contact again, reproductive isolation already exists between them, or becomes progressively established. The species originating from such a type of speciation can be separated only by a few " minor " genetic alterations, bearing only upon a few structural loci. The morphology of the two species can be very similar or even identical (notion of " sibling species " or dualspecies; see BERNARDI, 1980), and so can it be as regards the structure of their chromosomes, their behavior, their ecology, etc. (except eventually for some behavioral differences working as pre-ejaculatory mechanisms of isolation). These species often remain able to give birth to viable hybrids, at least in experimental conditions.

In the cases of speciation belonging to the second category, on the contrary, the genetic alterations are more important and sudden. Although they do not affect all the genotype as it had first been thought, the modifications can be of a different nature, since they can concern the genetic regulatory systems themselves, and not only the structural genes. Speciations of this type probably occur mainly in small isolated founder populations. They sometimes, but not always, produce species that are quite different in their morphologies, behaviors, ecologies, etc.

The two categories of speciation, the " gradual " one and the " quantic " one, are fundamentally distinct and occur in very different conditions. Moreover each of them includes several distinct modes of speciation (TEMPLETON, 1980 b, 1981, 1982).

Source : MNHN, Paris

Questions of terminology

How should one call the cases of sudden speciation that take place in small isolated founder populations, and in which the genotype undergoes a fundamental reorganization? Several terms have been proposed, which might suit this type of speciation: " transilience " (Galton, 1894; a term used again with a modified meaning by Templeton, 1979, 1980 a, 1980 b, 1981, 1982); " genetic revolution " (Mayr, 1954); speciation by " catastrophic selection " (Lewis, 1962); " quantum speciation " (Grant, 1963; phrase taken up by Stanley, 1979); " founder-flush speciation " (Powell, 1978); " regulatory revolution " (Templeton, 1979); " rapid speciation " and "saltational speciation " (Ayala, 1982); " founder-induced speciation " (Carson & Templeton, 1984); etc.

Assuredly, these various terms are not exactly synonymous with each other. Most of them were precisely coined by their authors because the *mechanisms* (in particular genetic ones) imagined for this type of speciation were different from those postulated by the previous authors. However, it is clear that the various concepts are akin, since they all describe cases of sudden speciation, in opposition to the phenomena of gradual and slow speciation which had long been considered as the only ones existing.

Mayr's (1954) phrase " genetic revolution " was used for a long time to indicate the cases of sudden speciation by founder effect in small isolated populations. Templeton (1979, 1980 a) having proposed the new term " genetic transilience ", elicited the following comment from Mayr (1982 a: 885-886):

> " Templeton assumed that his modified interpretation of genetic revolutions would require the introduction of a new term (' genetic transilience '). However, this change of interpretation is far less than between the species of Linnaeus, the gene of Johannsen, the mutation of de Vries, and the current concepts designated by these terms. We would drown in terminology if a new term were introduced every time a scientific concept was modified. Furthermore, Galton coined the term ' transilience ' for a major saltation in a single individual. "

I agree with Bernardi (1956, 1980) and Mayr (1982 a) that only the rule of priority should be used to choose between various " synonymous " terms. However, I think that the terms "transilience " and " genetic revolution " are not synonymous, but that the second one describes only one particular case among all the phenomena concerned by the first one. Similarly, " genetic revolution " is only one of the possible types of " peripatric speciation ", i.e. which occur in small isolated populations (Mayr, 1982 b, 1982 c).

Galton (1894: 368) defined the term *transilience* as opposed to *divergence* :

> " The phrase of organic stability must not as yet be taken to connote more than it actually denotes. Thus far it has been merely used to express the well-substantiated fact that a race does sometimes abruptly produce individuals who have a distinctly different typical centre, in the sense in which those words were defined. The inference or connotation is that no variation can establish itself unless it be of the character of a sport, that is, by a leap from one position of organic stability to another, or as we may phrase it, through ' *transilient* ' variation. If there be no such leap the variation is, so to speak, a mere bend or divergence from the parent form, towards which the off-spring in the next generation will tend to regress ; it may therefore be called a ' *divergent* ' variation. Thus the unqualified word variation comprises and confuses what I maintain to be two fundamentally different processes, that of transilience and that of divergence, and its use destroys the possibility of reasoning correctly in not a few important matters. The interval leapt over in a transilience may be at least as large as it

Source : MNHN, Paris

has been in any hitherto observed instance, and it may be smaller in any less degree. Still, whether it has been large or small, a leap has taken place into a new position of stability. "

Of course, as MAYR (1982 a, 1982 c) observes, the " genetic model " evoked by GALTON (1894), which consists of a sudden evolution by macromutation in a single individual, belongs to the same type as GOLDSCHMIDT's (1940), " hopeful monster " model, and it cannot be supported anymore today. However such a model was not absurd back in 1894, before MENDEL's laws were rediscovered and populations genetics was born. GALTON's (1894) merit was to make a distinction between two fundamental types of evolution — by divergence and by transilience. This distinction is still valid today, although other terms have sometimes been used to mark it: " phyletic gradualism " and " quantum evolution " (e.g.: SIMPSON, 1944, 1953; STANLEY, 1979), " geographic speciation " and " quantum speciation " (AYALA, 1982), etc. With TEMPLETON (1980 b, 1981, 1982), I deem that GALTON's (1894) terms *divergence* and *transilience* must be kept to name the two major categories of speciation modes.

Besides, as TEMPLETON (1980 b, 1981, 1982), has shown, the transilience category, just like that of divergence, is not homogeneous. This author distinguishes between four fundamental modes of speciation within the first category: " genetic transilience ", " chromosomal transilience ", "hybrid maintenance " and " hybrid recombination ". Some of these modes of speciation do not call for a founder population of small size in the least. For instance, speciation by polyploidization can occur in sympatry and in a single generation (see DUBOIS, 1977 b and BOGART, 1980), and yet the resulting polyploid species may have no allele different from the diploid species (or from the two diploid species, in the case of allopolyploidy) it derives from: the new polyploid species may produce perfectly viable hybrids with the ancestral diploid species, but these hybrids produce aneuploid gametes and their descent shows signs of deep chromosomal imbalance and is not viable (see e.g. DUBOIS, 1977 b: 195). In such cases it is clear that there was indeed speciation by " transilience ", but no " genetic revolution " at all. It is only after a long period of separation that the polyploid species and its ancestral species will have sufficiently diverged to manifest differences at the genic, and not only at the chromosomal, level.

Among the four types of transilience acknowledged by TEMPLETON (1980 b, 1981, 1982), only the one that he calls " genetic transilience ", and that CARSON & TEMPLETON (1984) later called " founder-induced speciation ", corresponds to the phenomenon we are here concerned with. Moreover, as we have seen, this category itself is not homogeneous. Obviously, the first term available for this category is speciation by *genetic revolution* (MAYR, 1954). I therefore suggest keeping this term to call one of the types, and one only, of the larger category of speciation by *transilience*. I propose to use this term in a strictly *descriptive* perspective, to describe sudden speciations in isolated populations, which does not imply an agreement with the model MAYR (1954) proposed in a purely speculative fashion to account for the *mechanism* at work in such speciations. When mechanisms are at stake, I deem it better to call them, as BARTON & CHARLESWORTH (1984), for example, do, by names such as " MAYR's (1954) model (or theory) ", " CARSON's (1975) model ", "TEMPLETON's (1980 a) model ", etc.

Although, according to the rules proposed by BERNARDI (1956, 1980), a term should not be rejected because it is " improper ", let us remark that the term " genetic revolution ", which was criticized in this respect, seems to me to have been very well chosen:

" It has been questioned, with some justification, whether the term ' revolution ' was not too strong. The student of history, however, knows that many revolutions hardly touched any other institution of a country except the form of its government. Furthermore, nothing ever occurs in other kinds of populations that even approaches the drastic genetic turnover of those founder populations that experience a genetic revolution. " (MAYR, 1982 b: 1124).

Source : MNHN, Paris

Moreover, GOULD & ELDREDGE (1977) are obviously right when they account for the resistance of many biologists to the notion of quantum evolution, and particularly to the theory of genetic revolution, in terms of ideological factors, and I associate myself with their plea in favor of a " general philosophy of change ":

> " We believe that a coherent, punctuational theory, fully consistent with Darwinism (though not with DARWIN's own unnecessary preference for gradualism), will be forged from a study of the genetics of regulation, supported by the resurrection of long-neglected data on the relationship between ontogeny and phylogeny (see GOULD 1977). AGER (1973, p. 100) (...) speaks in simile of the tempo that we support as most characteristic of the way our world works: ' The history of any one part of the earth, like the life of a soldier, consists of long periods of boredom and short periods of terror '. " (GOULD & ELDREDGE, 1977: 147).

GENETIC REVOLUTION AND GENIATION

As we have just seen, it is now clear that there is not one, but several, modes of speciation. There is also good reason to think there must exist several modalities of speciation by genetic revolution: CARSON's (1975, 1982) and TEMPLETON's (1980 a) models already present two possibilities (CARSON & TEMPLETON, 1984). Without further speculation on these models of populations genetics, which I think premature, I would like, by way of conclusion, to grant some reflection to the relations that may exist between genetic revolution and geniation.

Let me stress first that I do not think that the two phenomena are always linked. In other words, I think: (1) that there can occur a genetic revolution followed by a " simple speciation ", without appearance of a new genus; (2) that, in some cases, a new genus can appear progressively, gradually, in particular in a lineage submitted to a strong rate of anagenesis. However I consider that (3) *in most cases*, geniation occurs on the occasion of a genetic revolution. I therefore consider that even if the two fundamental types of geniation (by divergence and by transilience) exist, the latter is much more frequent than the former.

The fundamental distinction that I think separates geniation from " simple speciation " is the fact that in the latter the modifications of the genotype bear solely, or mainly, upon structural genes, whereas in geniation they affect mainly regulatory genes (CARSON's (1975, 1982) and SENE & CARSON's (1977) " closed " genetic system).

The fact that the modification of the genetic regulatory systems may lead to radical alterations in the genic expression (in particular during the development), and therefore in the characteristics of the morphogenesis and, lastly, in the adults' morphology, physiology and ecology, has been mentioned several times here above. It has been discussed in detail in RAFF & KAUFMAN's (1983) work. They insist upon the fact that regulatory genes, which play a great evolutionary rôle, are in relatively small number: therefore, the fixation, on the occasion of a genetic revolution, of one, or only some, mutations bearing upon such genes, in an isolated founder population of small size, may prove sufficient to lead to a " decoupled " change, in LEMEN & FREEMAN's (1984) sense, and to the passage into a new adaptive zone.

In the light of what precedes, the following can be asserted:

(1) The birth of a new genus is not a simple and frequent event, because of both genetic and developmental constraints, and of ecological constraints. The constraints of the first type have been known for a long time, and expressed through concepts such as canalization, coadaptation, epistasy, etc. They have been evoked from various viewpoints, for instance in MAYR's (1975, 1982 b) discussions on the " unity " or "cohesion " of the genotype, in CARSON's (1975, 1982) discussions on the notion of " closed " genetic system, in ALBERCH's (1980, 1982), WAKE (1982 a, 1982 b), WAKE, ROTH & WAKE's (1983) and many

Source : MNHN, Paris

others' discussions on the rôle of developmental constraints in evolutionary processes, etc. These constraints are examined in detail in RAFF & KAUFMAN's (1983) book. As for the ecological constraints, they are mentioned for instance in SIMPSON's (1944, 1953) works on the discontinuity of adaptive zones, separated by nonadaptive zones.

(2) Because of these constraints, the birth of a new genus is likely mainly in exceptional conditions. These conditions can be met with in a founder population of small size submitted to a new environment: there can then occur a genetic revolution, in which the " cohesion of the genotype " is broken, the " closed " genetic system decoupled by recombination or by mutation, and the systems of genetic regulation profoundly altered and reorganized. The phenomenon of genetic revolution takes place on the scale of a population and not on that of an isolated individual. It consists in the fixation, by populations genetics' phenomena (selection, adaptation, etc.), i.e. gradual, even if rapid, of new regulatory genes or of new modalities of interaction between those genes. The model proposed for this process reconciles the molecular, developmental and populational approaches of evolutionary processes.

(3) Not all genetic revolutions give birth to a new genus, but some do.

PASTEUR (1982) proposed distinguishing between two types of events due to founder effects: one, for which he uses the term genetic transilience, would be sudden, almost instantaneous; the other, which he calls genetic revolution, would spread out more in time. He suggested that the birth of a new genus would require a process of genetic revolution extended over a long span of time, making it possible to bridge the gap between two adaptive zones. For this process, he proposed the term " hopeful transilience " (PASTEUR, 1982). As an illustration, he gives the convincing example of the Malagasy gekkonid genus *Millotisaurus*, for which he had used, as early as his work back in 1964, whose discussion is worth re-reading, the Simpsonian phrase "quantum genesis of a taxon of higher category " (PASTEUR, 1964: 105).

However we need not necessarily call for a long phase of instability in order to explain all the cases of founder geniation. The particularity of genetic revolution is precisely that is dissociates the " closed " genetic system and makes the reconstruction of a new coadapted genetic complex possible, so that precisely this process enables the rapid passage from one adaptive zone to another, without any " lingering " in the intermediate inadaptive zones. Moreover, as CARSON (1982) stresses, young species, which have not had time to reconstruct a " closed " genetic system, are more likely than others to re-enter phases of imbalance leading to new speciations:

> " It may well be that an old mature species becomes so locked into obligatory balances that this condition is not conducive to the formation of new species, since the genetic system is resistant to the disorganization phase. Such old species thus may not be competent for the budding off of new ones; they may be looked upon as having essentially become inert from the evolutionary point of view.
>
> Conversely, a fairly young species that has perhaps been through only several thousand generations of organizational balance may be capable of early budding off populations capable of disorganization and reorganization. This may account for the repeated observation, in the contemporary fauna and flora, of clusters of very closely related species (' explosive speciation '). I refer to species clusters found in some freshwater lakes (eg Lake Baikal) or species in clusters such as are found in Hawaiian drosophilids. " (CARSON, 1982: 425).

For the appearance of *Millotisaurus* as for that of other similar cases, we must therefore suppose a series of speciations by successive genetic revolutions rather than a long period of imbalance " between " two genera.

The genetic revolutions that occur in the geniation process must be of a particular type, or " important " enough in terms of genetic rearrangements, to have the three following consequences, which characterize the birth of a new genus (according to the genus conception that was developed here above): (a) change in morphology, in which the " shape " factor happens to be decoupled from the " size " factor for a

Source : MNHN, Paris

while (" decoupled event " of LEMEN & FREEMAN, 1984); (b) postzygotic genetic isolation from the ancestral species, with which hybridization becomes impossible, because of the incompatibility of the genetic systems of the two species during the development of the hybrid embryo; (c) change in other dimensions of the holomorph, in particular change of ecology and passage into a new adaptive zone. I consider these three phenomena not to be independent processes, but, together, the results of one event of "genetic revolution ". These three characteristics make geniation differ from " simple speciation ", i.e. phenomena of speciation that only lead to a multiplication of species within the same genus, which corresponds to what LEMEN & FREEMAN (1984: 1234) call " diversification in size within one shape group ". " Simple speciation " is not accompanied by as important a change in morphology and ecology as that which separates two genera after my definition. In some instances, the loss of the ability to hybridize can occur during events of "simple speciation ": that is not in contradiction with what precedes, insofar as the inability of two species to hybridize may be caused by a few genetic factors only, sometimes by only one gene. This inability has therefore no particular evolutionary or systematic meaning. Conversely, the fact that two species should remain susceptible of giving birth to viable adult hybrids testifies to the fact that their systems of genetic regulation have remained compatible, therefore very akin, so that the two species still belong to the same genus.

(4) We have seen that, in a synthetic conception of classification, genera can be defined by three types of criteria, which represent the three sides of the same reality: genetic, phylogenetic and ecological units as they are, genera are evolutionary units which exist as such in nature. In the light of what precedes, the genus appears as a basic category, which expresses the fact that a species has left the adaptive zone of the ancestral species and has begun to conquer a new milieu. Thus the genus is the first of the higher categories, and not only a " group of related species ". Genera so defined are both clades and grades. The birth of a new genus is a phenomenon that is qualitatively different from " simple speciation ": once a species has crossed a " gap " of adaptive imbalance and " landed " in a new adaptive zone, there may occur a new explosion of speciation. In this respect, and first under the form of *one species only*, the genus is "preexistent " to the species that will constitute it; its appearance will enable their multiplying. After the arrival in the new grade, radiation may give birth to better and better adapted species, and the ancestral species of the genus may disappear, though it made ulterior speciation possible. In this respect each genus clearly is a *natural* taxon, expressing the existence of a real phenomenon in nature (see also SCHAEFER, 1976).

(5) Genera so conceived can have an extremely variable size, some being monotypic, others being very large (several hundreds or even thousands species). Rather than trying to artificially break up the genera that are " too large " and group together the genera that are " too small ", for instance by requiring that the size of the " gaps " separating genera be inversely proportional to the size of the latter (MAYR, LINSLEY & USINGER, 1953; MAYR, 1969), I think this disparity must be respected, for it expresses a real phenomenon. The " large " genera are those that have " succeeded ", that have conquered a large adaptive zone. The small ones on the contrary are in adaptive zones that are either narrower or already partly occupied by species of a different phylogenetic origin. We would considerably deprive the notion of genus of its meaning if we systematically broke up large genera. It is then useful to acknowledge taxinomic sub-units within genera: the next chapter of this work gives them a brief look.

Source : MNHN, Paris

Conclusion

Although this paper deals mainly with the discussion of the criteria one can use to recognize genera in zoology, and in particular the new criterion of hybridizability, I have felt it useful to study the mechanisms likely to account for the geniation process. The forerunning discussion is based upon the present state of our knowledge about animal speciation: as we have seen, it is grossly incomplete, and the share of hypotheses is still important. Part of these may well have to be altered, or even totally abandoned in the future. Let us stress however that these possible modifications should not invalidate my main propositions. In other words, if it is true that the criterion of hybridizability to define genera has the advantage of being in agreement with the model of geniation proposed above (which I think grants it its biological and evolutionary value), the two can however be disconnected: it is not necessary to accept this model of geniation to accept the criterion of hybridizability, which entails many practical advantages, independently from the biological and evolutionary meaning I gave it. Such an agreement is not necessary either to accept the term *geniation*: this term is purely descriptive; it designates an undeniable evolutionary phenomenon, whatever the models proposed to account for it may be. If we agree with Gould & Eldredge (1977: 139)

> " that the importance of a phenomenon is not recognized unless it has a special name ",

we must then admit that the lack, until 1981, of a proper term to describe the birth of a new genus testifies to the lack of interest among evolutionists for this type of events until today: I hope that the present work will incite new reflections and studies in this respect.

Source : MNHN, Paris

Source : MNHN, Paris

THE TAXINOMIC CATEGORIES BETWEEN THE GENUS AND THE SPECIES

SUPERSPECIES, ULTRASPECIES AND SUPRASPECIES

It is not useful to return here to the definition, the history and the synonymy of the categories *superspecies* and *ultraspecies*, which were very clearly discussed by BERNARDI (1980). This author showed that the many categories created in the past by systematists to take place between the subgenus and the species could be reduced to a few only, of which MAYR's superspecies (a group of BIRULA's prospecies) and KIRIAKOFF's ultraspecies (a group of PRYER's dualspecies) are the two most important ones. Let us hope that this review will be accepted as an authority and that, starting from this work, all systematists and evolutionists will use the same words for the same phenomena.

The purpose of BERNARDI's work is

> " to transform taxinomic categories into a tool for the study of evolution instead of being an obstacle to this study. " (BERNARDI, 1962: 333; translation mine).

For the same reason it is necessary to recognize, between the genus and the species, several categories, which do not necessarily fit into each other as is the case in the rest of the Linnaean hierarchy: it is thus perfectly possible for a group of species to be both a superspecies and an ultraspecies.

In the same book in which BERNARDI's (1980) paper appears, GÉNERMONT & LAMOTTE (1980) proposed a new supraspecific and infrasubgeneric category, that of *supraspecies*, which groups in fact all the supraspecific categories defined by BERNARDI (1980). The proposal of these authors is therefore in opposition to that of BERNARDI (1980): they suggest grouping under a same name, in a same category, sets of species which represent very different evolutionary phenomena, instead of reserving a distinct term to each of these phenomena. GÉNERMONT & LAMOTTE's (1980) superspecies is a taxinomic category which is devoid of precise evolutionary meaning and which principally has a " practical " interest. While the use of the categories discussed by BERNARDI (1980) should prompt authors to refine their analysis of evolutionary phenomena as much as possible, the use of the supraspecies would rather tend to discourage such an enterprise, and for this reason does not seem advisable.

Source : MNHN, Paris

Species complex and species group

For the evolutionist, the most interesting of the categories situated immediately above the species is certainly that of the superspecies. Very schematically, one may conceive the superspecies as follows: when a species has a relatively vast area distribution, and when the latter is subdivided into several discontinuous zones, there may occur a divergent evolution, in allopatry, of the various sets of populations; these may remain members of a single species, of which they constitute the subspecies, but they may also reach specific status. These various sets of populations may then be designated as the prospecies of a single superspecies. When a secondary contact zone appears between two prospecies, a " zone of overlap and hybridization " may become established in this region, and from that moment the two species have a parapatric distribution (see e.g. Dubois, 1977 b).

The parapatric distribution is maintained as such, during a certain time, thanks to mechanisms which are often poorly known: it seems that the simple presence of each species may be the proper barrier which precludes the other one from spreading beyond the zone of contact. But this is a transitory situation, which cannot persist during long geological periods. Two fundamental sorts of evolution may occur then: either the two species continue to exclude each other mutually in the regions that they occupy, but the contact zone between them progressively moves, until one of the two species, rejected against a natural barrier, is eliminated (Dubois, 1977 b: 173); or the genetic and eco-behavioral divergence between the two species increases, progressively allowing these species to become sympatric, at least in certain regions.

In this latter case, it is no longer possible to speak of superspecies. It is then possible to speak of *species complex* or of *species group*. These two categories are often used indiscriminately, in a relatively informal way, by various authors. It seems to me however that it could be useful to apply these categories to two slightly different evolutionary situations, and by doing so to go further into the work of terminological clarification started by Bernardi (1980).

The species complex could correspond to the first evolutionary stage which comes after the superspecies once a (at least partial) sympatry has been established between two (or several) species. At this stage hybridization may still occur, albeit rather exceptionally, in nature. Let us however note that the hybrids obtained are then either nonviable, or sterile, and are therefore not at the origin of an effective gene flow (with introgression) between the two species, for otherwise we would be in the situation of having two entities which have not really reached the status of species but which correspond to what Bernardi (1980) calls quasispecies or vicespecies.

Afterwards, natural hybridization tends to disappear, to be totally or almost totally absent in the case of the species group, of which furthermore the species may be largely sympatric, and may not retain much trace of their previous allopatric or parapatric distribution. The species of a species group, however, still remain morphologically very similar to the unique ancestral species from which they descend, which gives them this " family likeness " mentioned by Pasteur (1964: 118), who further remarks that species groups

> " are entities having essentially a phylogenetic meaning which may not be utilizable for determination: they can be defined positively by the affinities which connect certain species one with another, but not dichotomically and negatively by diagnostic criteria; they may not necessarily be discriminated one from another in an absolute way. " (Pasteur, 1964: 97; translation mine).

Source : MNHN, Paris

Several degrees of complexification exist, after additional speciations within a group, and, in a purely practical aim, it may be useful to recognize additional subdivisions: species subgroup, super-group, etc. (see e.g. DUBOIS, 1976, 1977 c; DUBOIS & KHAN, 1980; DUBOIS & MATSUI, 1983). These various categories have no formal status in systematics and are only useful conventions.

Species groups are much less diversified taxa than genera. Just as a species having a large distribution may be subdivided into subspecies, a genus having a large distribution may be subdivided into species groups. Species groups are formed more often, but not always, in allopatry: they correspond then to a geographical differentiation within a genus. But if the adaptive zone of the genus does not show major changes in the whole area of the genus, there will occur little divergence between the species groups, in particular no ecological divergence, each group playing a similar rôle in each region. A good example in this respect is the cosmopolitan genus of anuran amphibians *Bufo* (BLAIR, 1972 a).

Any speciation implies however a certain ecological divergence, at the level of the species, allowing several species groups to become sympatric. The number of species groups sympatric in a given region remains however limited, as is also illustrated here by the genus *Bufo* (BLAIR, 1972 a).

It may be useful to briefly discuss the mode of notation of the different categories of evolutionary taxinomy which have just been mentioned. At the moment, any author who wants to express the fact that a species belongs to a species complex or to a species group is obliged to have recourse to a periphrase, of the type: " *Rana palustris*, of the *Rana pipiens* group ". The mode of notation exposed by BERNARDI (1980: 413-414), and which was recently integrated in the *International Code of Zoological Nomenclature* (ANONYMOUS, 1985), allows one to lighten this notation. The preceding example could thus be written: *Rana* (gr. *pipiens*) *palustris*. The four supraspecific and infrasubgeneric categories briefly discussed above could be distinguished, in such a notation, by the use within parenthesis of one of the four following abbreviations: supersp. for superspecies, cplx. for species complex, gr. for species group, and ultrasp. for ultraspecies.

SYNKLEPTON

In the last twenty years, various works have demonstrated the existence in nature of particular animal " forms " which cannot be considered as " true species ", such as the unisexual, gynogenetic and hybridogenetic forms of fishes of the genera *Poeciliopsis* and *Poecilia* (see e.g. SCHULTZ, 1977), and the hybridogenetic forms of anurans of the genus *Rana* (see e.g. DUBOIS, 1977 b, 1982 c).

All these forms, despite their diversity, have the following characteristics in common:

(1) They are of hybrid origin. Some of them derive from hybridizations between two " good " species, others from hybridizations between a " good " species and a hybrid form.

(2) These forms do not behave genetically like " good " species, but have the genetic characteristics of clones. Hybridogenetic forms are hemiclones, and gynogenetic forms are full clones.

(3) These forms cannot survive alone in nature. They need to " steal " gametes from " good " species to realize their reproduction, thus having recourse to a kind of " sexual parasitism ".

Insisting upon the fact that such forms cannot be considered as true " biological species " (which reproduce and evolve independently one from another, and are characterized by a biparental sexual reproduction, with a genic flow which is potentially free between all members of the species, recombinations between the parental genomes during the meiosis, etc.), DUBOIS & GÜNTHER (1982) proposed giving such forms the name of *kleptons*, and to call *synkleptons* the

Source : MNHN, Paris

groups consisting of two " good species " (or more) and one (or several) klepton(s) issued from the hybridization of these species. They proposed considering kleptons as taxa of the species-group, belonging to a third taxinomic category distinct from that of species and of subspecies, and they suggested rules for the nomenclature of these forms. Thus, within the *esculenta* synklepton of the genus *Rana*, occurring in all Europe, where it consists of more than ten distinct species and kleptons (DUBOIS, 1982 c), and where furthermore several different types of populations do exist (GÜNTHER, 1983), the names suggested for the various existing forms are of the type *Rana* (synkl. *esculenta*) *lessonae* for the species, and *Rana* (synkl. *esculenta*) kl. *esculenta* for the kleptons.

Synkleptons and kleptons are undeniable evolutionary units in nature: they are phylogenetic and genetic units (within which genetic exchanges continue to occur between separated forms) and ecological units (see DUBOIS & GÜNTHER, 1982). Kleptons may persist as such in nature for long periods (sometimes thousands of years), but they are not necessarily evolutionary dead-ends: they may constitute intermediate stages leading to other forms, such as polyploid bisexual " good " species (see in particular DUBOIS, 1977 b, and BOGART, 1980).

For the time being, kleptons and synkleptons are known with certainty only in vertebrates, but, as we have suggested (DUBOIS & GÜNTHER, 1982), it is very possible that similar situations also exist in invertebrates, where they have not yet been recognized as such. It is likely that these situations are much more abundant in nature than it has been believed until now, and that various groups considered until now as " species groups " will prove in the future to be synkleptons, composed of " good " species and of kleptons.

THE SUBGENUS

INTRODUCTION

Although it is officially recognized in the *International Code of Zoological Nomenclature* (ANONYMOUS, 1985), the subgenus category is used in a very unequal way in the different branches of zoology. For many authors, it is only a " small genus " or a " large species group ". The subgenus is rejected by some authors, in particular those who consider embarrassing the presence of a Latin name, which is later liable to be elevated to generic rank (DUNN, 1943; DUELLMAN, 1977). Such a conception seems to imply that it is classification which reflects nomenclature, not the reverse, which is inacceptable in theory and very disturbing if it happens in practice.

Within the framework of the definition of the genus here proposed, it seems that the subgenus may be conceived as a category distinct from both the genus and the species group, and which would allow one to underline the existence of evolutionary phenomena of a different type. To illustrate these differences in concrete terms, I will largely make use of examples from the amphibians.

The subgenus could be used in two particular situations:

(1) It first seems indicated to recognize subgenera when one can detect, within a genus, a manifest tendency towards progressive *improvement* or *refinement* of the adaptation of the species to the adaptive zone of the genus: the first species " landing " in the zone are still rather poorly adapted to it, the following ones are more finely adapted. There may then exist a tendency to the replacement of the first ones by the following ones (the subgenera being then successive), just as it is possible, in certain conditions, that two subgenera should subsist together, possibly in different regions. A good example of

Source : MNHN, Paris

this is that of the two subgenera of the Asiatic genus of anuran amphibians *Scutiger*, which show two successive stages, which by the way are not clearly separated by a discontinuity, in the adaptation to life in high altitude torrents (DUBOIS, 1979 a, 1980 b).

(2) A second case where the notion of subgenus may apply is that where the adaptive zone of a genus is *large* or *diverstified* enough to allow a subdivision into several adjacent subzones, in which species groups *specialize* (which does not exclude other species or species groups from retaining a less specialized ecology, which may cover the whole adaptive zone or several subzones). These subgenera are then contemporaneous and sometimes sympatric, sharing among them resources and niches. A good example in this case is the genus *Rana*, the adaptive zone of which is exceptionally wide and has become divided into several subzones, which correspond to as many subgenera (BOULENGER, 1918, 1920; DUBOIS, 1975, 1976, 1981 b, 1984 a, 1984 c).

This specialization within a zone, which implies no discontinuity, is distinct from the shift to a different zone. It is possible to postulate (DUBOIS, 1975, 1976, 1981 c, 1982 a) that, in this case, the genetic changes which have occurred are minor and therefore possibly *reversible*, that these changes would not constitute a real genetic revolution.

THE CRITERIA OF THE SUBGENUS

Distinction between subgenus and genus

Such a conception of the subgenus entails the possibility of using three types of criteria to distinguish subgenus from genus.

Hybridizability

The species of various subgenera of a same genus, although they may exhibit relatively important differences between them as far as morphology and ecology are concerned, may be liable to give viable adult hybrids. The use of this criterion of *hybridizability*, which was dicussed at length above, would allow one to definitely resolve many systematic problems which have long divided the authors. As a matter of fact, many cases do exist where it is clear that two groups of species are very close, but at the same time show significant differences. Such cases are not rare in particular in amphibians where furthermore, starting with NOBLE (1924), the subgenus category has fallen into disgrace. Workers are then confronted with the following alternative: either two genera, or two species groups, should be recognized. With some authors insisting upon the differences and others on the resemblances, one has often observed, without any justification due to the discovery of new facts, vacillation between these two attitudes, which is deleterious to the stability of nomenclature. In many cases, the intermediate attitude, which consists in considering the two groups as subgenera of a same genus, seems best able to solve the problem, in asserting at the same time both the resemblance (same genus) and the difference (different subgenera).

A very good example of this is that of the problem of the status of the American " tree frogs " grouped under the name *Pseudacris* (see DUBOIS, 1982 a, 1984 b). This name has long been used in northern America and for this reason authors conserve it as a generic name, although the characters which separate *Pseudacris* from *Hyla* are very weak. Thus DUELLMAN (1970: 642) writes:

> " The frogs of the genus *Pseudacris* differ from most North and Middle American *Hyla* by having small discs and greatly reduced webbing on the feet. No other external features will distinguish them from *Hyla*. If these frogs occurred in South America, they probably would not have been recognized generically. "

Source : MNHN, Paris

As a matter of fact, the species grouped under *Pseudacris* are obviously phylogenetically close to certain species groups of *Hyla*, as is shown by the study of mating calls (BLAIR, 1958, 1959), of osteology (GAUDIN, 1974) and of albumins (MAXSON & WILSON, 1975), as well as the fact that some species combinations may give hybrids (RALIN, 1970). However it is true that *Pseudacris* has a different overall morphology and a peculiar type of ecology, these species being described as " terrestrial " or " terrestrial-fossorial " by RALIN (1970: 44). There exist therefore good arguments to consider that these species *are* members of the genus *Hyla* and that they are " not like other " members of this genus. It appears therefore very justified to treat *Pseudacris* as a subgenus of *Hyla*, which until now, despite abundant discussions on the problem of " the validity of *Pseudacris* ", no author seems to have contemplated doing, the problem being always set in terms of the wrong alternative: " it is a genus or nothing ".

A second example may be borrowed from the urodelan amphibians, in which the success of the hybridization between the European species *Pleurodeles waltl* and the Asiatic species *Tylototriton verrucosus* (FERRIER, BEETSCHEN & JAYLET, 1971) is enough in itself to consider, in my opinion, the two contemporaneous species of *Pleurodeles* and the four species of *Tylototriton* (THORN, 1969; NUSSBAUM & BRODIE, 1982) as belonging to a single genus *Pleurodeles*, although to two distinct subgenera, to which a third subgenus *Echinotriton* should be added (see NUSSBAUM & BRODIE, 1982; FROST, 1985; DUBOIS, 1987 b).

Evolutionary reversibility of characters

A second interesting criterion is that of the evolutionary *reversibility* of adaptive characters. The fact that this reversibility remains possible indicates that these characters are determined by a very small number of genes, possibly by a single regulatory gene. Some examples may be found in this respect among amphibians.

The presence or absence of digital discs has long been considered as an important character, allowing to define genera, if not families, of anurans. However it is easy to notice that such discs appeared independently and in parallel in several lineages of anurans. Species of a same genus, sometimes very close to each other, may differ between themselves in this character: thus some species are " intermediate " in this respect between the subgenera *Rana* and *Hylarana* of the genus *Rana* (BOULENGER, 1920), or some species which obviously belong to the subgenus *Hylarana*, like *Rana galamensis* and *Rana darlingi* in Africa (LAURENT, 1956) or like *Rana malabarica* in Asia (DUBOIS, 1981 b) are devoid of discs. It seems that a single mutation or a very low number of mutations may be enough to determine the presence of terminal dilatations at the tips of digits and toes in a species which is usually devoid of such dilatations (SMITH & LIST, 1951). Even if, as is probably the case, such " dilatations " are not identical with true discs, it seems clear that the presence or absence of discs is in anurans a very labile character, liable to appear or disappear independently in different lineages, and which cannot in itself be used to separate genera.

Similarly, the presence of intercalary phalanges, although considered by some authors as an adequate feature with which families of anurans may be defined, also seems a character of little interest, since supernumerary phalanges may appear as anomalies in species which do not usually have them (DUBOIS, 1974 b). The same is true for the presence of nuptial spines on the breast and forearms of reproductive males, these characters having appeared independently in various families and being liable to lack in species very close to species which have them, as is the case with the almost sibling species *Rana liebigii* and *Rana vicina* (DUBOIS, 1980 a). Let us finally cite the absence of a toe on the hind limbs, which has sometimes been considered as a generic character, e.g. for separating *Salamandrella* from *Hynobius*, while ectrodactyly may occur in some populations of *Hynobius* (MARUYAMA, 1977) and that it is known to be, in some cases, of a simple, monogenic, determinism, in amphibians (DUBOIS, 1977 a).

The criterion of reversibility may also considered in a negative way. It is clear that certain morphological characters or certain ecological, physiological, etc., adaptations, depend on a complex genetic determinism and do not allow a true reversibility, i.e. a simple return to conditions strictly identical to the ancestral, plesiomorphous, conditions, which would imply, so to speak, a " genetic counter-revolution ". Thus the ventral sucker of the rheophilous tadpoles of the genus *Amolops* (INGER, 1954, 1966) does not

Source : MNHN, Paris

seem liable to be lost at little cost and it may be supposed that the tadpole of a species issued from the genus *Amolops* but which would have secondarily returned to a non-torrenticolous mode of life would keep some trace of the very peculiar morphology of its close ancestors, and at any rate would very probably exhibit appreciable differences with the tadpoles of the genus *Rana*, from which the genus *Amolops* is probably issued (DUBOIS, 1982 a; see also KURAMOTO, WANG & YÜ, 1984).

Another interesting example in this respect is that of the African anurans currently grouped in the genus *Nectophrynoides* (GRANDISON, 1978). This set of species obviously constitutes a homophyletic unit, separated by a marked morphological " gap " from the genus *Bufo* and the other genera of bufonids (GRANDISON, 1978). However, despite the low number of species of this group currently known, these show a great diversity of types of reproduction and of development, which may be classed in four major categories (GRANDISON, 1978; WAKE, 1980). These four groups show between them differences which most likely translate important and irreversible genetic changes, and it seems necessary to account for this important phenomenon by subdividing this group into four distinct genera (DUBOIS, 1982 a, 1987 b): a first one would correspond to *N. osgoodi*, which lays numerous small pigmented eggs in water, which give birth to tadpoles of the " generalized " type (GRANDISON, 1978); a second genus would contain *N. malcolmi*, which lays large, not numerous, unpigmented eggs on the ground, and the development of which takes place out of water (GRANDISON, 1978); a third genus, which would keep the name *Nectophrynoides*, would group the ovoviviparous species like *N. tornieri* and *N. viviparus*, with large, but not numerous, eggs (LAMOTTE & XAVIER, 1972; LAMOTTE & LESCURE, 1977); finally, a fourth genus would accomodate the viviparous species *N. occidentalis* and *N. liberiensis*, with few small eggs (LAMOTTE & LESCURE, 1977; XAVIER, 1979). Nothing opposes the creation of a subfamily Tornieriobatinae (DUBOIS, 1982 a, 1983 b, 1984 d, 1985 a, 1987 b), grouping the four genera above and the related genera, and emphasizing the fact that they constitute, within the Bufonidae, a homophyletic group, but of a higher rank than that of genus. Many other examples of this type could be mentioned.

Absence of discontinuities between subgenera

A third and last criterion is the *absence of discontinuities* between subgenera. It is not rare to find species intermediate between two subgenera, difficult to class and which must be rather arbitrarily attached to one of them. The discovery of such species may lead one to consider two groups of species which had until then been considered as distinct genera as subgenera of a single genus: this was the case for example in anurans of the subgenera *Scutiger* and *Oreolalax* of the genus *Scutiger* (DUBOIS, 1979 a, 1980 b).

Distinction between subgenus and species group

As for this second distinction, it does not rely at all on a question of size of the taxon (number of included species). A genus may be composed either of subgenera, or of species groups, or both, or neither (see e.g. ROSEN & BAILEY, 1963). The choice between the two categories implies, in the present perspective, a value judgement about the type of evolution which gave birth to the group in question. If only phenomena of cladogenesis (speciation), within a given adaptive zone, have occurred, one will speak of species groups. If phenomena of anagenesis (differentiation) also have occurred, and in particular if that implies an ecological specialization, it will be more justified to recognize subgenera. The large genera of anurans are exemplary in this respect: while *Bufo* and *Hyperolius* only contain species groups, ecological and morphological differentiation is on the other hand much more accentuated within genera like *Rana* and *Hyla*, where it seems justified to recognize subgenera, as was done by BOULENGER (1918, 1920), DUBOIS (1975, 1976, 1981 b, 1984 a, 1984 e, 1987 b) and others for *Rana*, but as has still apparently never been done for *Hyla*, despite the interesting remarks of MARTIN & WATSON (1971), who did not clearly consider this possibility.

While species groups, which have similar ecologies, are rather rarely sympatric, subgenera, being specialized, may easily become sympatric over vast regions: this is the case for several subgenera of *Rana* in Europe and in Asia.

Because they are adaptive, the characters of a subgenus will often be " good " taxinomic char-

Source : MNHN, Paris

acters, which may be used e.g. in dichotomic keys and in allowing an easy identification of specimens (PASTEUR, 1964: 97). However, and in particular because of the reversibility of characters, it will not always be the case: subgenera like genera may be polythetic.

At the level of the subgenus it may be difficult to ascertain if true homophyly is involved or if evolutive parallelism has occurred. Thus the " grade " *Hylarana* may have originated several times, in Asia, from the " grade " *Rana* s. str., giving birth to the various species groups of the subgenus *Hylarana* (BOULENGER, 1920; DUBOIS, 1981 a, 1982 a). It is certainly necessary to break up subgenera which prove to be artificial because they are polyphyletic; however this problem is less serious at this level than at the level of the genus, because the subgenus, contrary to the genus, expresses a *tendency* more than a *break*.

NOMENCLATURAL INTEREST OF THE SUBGENUS

The subgenus presents several nomenclatural advantages which seem to have, at least in part, escaped many systematists, in particular among the specialists of amphibians, although they have been stressed by a few authors (METCALF, 1915; SCHENCK, 1937; SIMPSON, 1943; EDWARDS, 1953; CROWSON, 1970; DUBOIS, 1981 c, 1982 a, 1984 e; etc.).

(1) First of all, the subgenus is *conservative*. It allows one to conserve particularly well-known old names. This would be the case e.g. if one was led, to satisfy the hybridizability criterion, to suppress several current genera of birds or of bony fishes: the names of these older genera could be kept, at least in part, for subgenera.

(2) The use of the subgeneric name, when one designates a species, is *optional*. This name must be used in purely systematic or faunistic works, and may also be used to designate, for instance, an interesting ecological unit in a work of ecology. This name must be totally omitted in works which are far from these concerns: works of embryology, physiology, biochemistry, etc., for which it is mostly important to know the generic group to which the species studied belongs (see ROSEN & BAILEY, 1963). The subgeneric name may also be deliberately omitted in systematic works, when the allocation of a species to a given subgenus poses some problems, e.g. nomenclatural ones (see DUBOIS, 1977 c).

In some revisions, an author may be led to provisionally subdivide a subgenus into several subgenera, without always being certain of the validity of some of them (e.g. because of the lack of certain types of information on certain species at the time of the revision). If available names do exist for these subgenera, it is possible to use them, but otherwise one must avoid creating names as long as the validity of the subgenera has not been demonstrated by good arguments. This does not raise any nomenclatural problem since only the generic and specific names are nomenclaturally indispensable.

(3) Finally, the subgeneric name is a unique, *collective*, Latin name. It allows one to designate a group by a name, without having at any time to describe or qualify it. This may be very useful when, e.g. in a work of systematic revision, this group must be designated as such dozens of times in the text (see e.g. DUBOIS, 1976). This simplification of writing is, let us not forget, the fundamental ground for a existence for a nomenclature like Linnaean nomenclature.

MAYR (1969: 197) has suggested that when a systematist hesitates as to the status to ascribe to two allopatric groups of populations (species or subspecies?), he should choose the status of subspecies. Similarly, when one hesitates as to the status of a group of species (genus or subgenus?), it seems indicated to consider it as a subgenus. As a matter of fact, this attitude is conservative, allowing one to provisionally keep the two names if they exist. Such a process indicates at the same time both broad groups to which are referred the species, and the existence of a divergence; it is liable to stimulate more thorough research on the relationships between the two groups (DUBOIS, 1982 a, 1984 e).

Source : MNHN, Paris

Conclusion

The hierarchy genus/subgenus/species group is by no means compulsory. Large genera may allow no subdivision, while very small genera may contain subgenera. Among the various Latin names which may appear in the designation of a form (names of subspecies, species, species group, subgenus, etc.), the generic and specific names remain the two most important ones and the only ones to be indispensable in all cases. The complexification of binomial nomenclature expresses the increase in our knowledge, but it should not lead us to forget that the Linnaean binomial remains the most important name, in particular for non-systematists, to whom systematics must bring useful information. In accepting a rather " broad " concept of the genus, we give pre-eminence to the major discontinuities: for a non-systematist, the distinction between *Rana* and *Platymantis* (characterized by its " terrestrial " development) or between *Rana* and *Amolops* (characterized by its very peculiar tadpole) is more important than those between *Rana* and *Hylarana* (Inger, 1954, 1966) or between *Scutiger* and *Oreolalax* (Dubois, 1979 a, 1980 b), because between these latter groups no clear discontinuity exists. This difference must be accounted for in the classification.

Source : MNHN, Paris

Acknowledgements

For the various helps they brought me in the preparation of this paper, I am most grateful to John C. Avise (Athens), Roger Bour (Paris), Jacques Daget (Paris), Pierre Dubois (Moulins), Carl Gans (Ann Arbor), Jean-Jacques Morère (Paris), Annemarie Ohler (Paris), Georges and Nicole Pasteur (Montpellier), Dominique Payen (Paris), Luc Plateaux (Paris), Denise and Donald Russell (Paris), Louis Thaler (Montpellier), Simon Tillier (Paris), Marie-Noëlle Uhl (Paris), Gregory S. Whitt (Urbana) and Émile Zuckerkandl (Menlo Park).

Paris, 7 November 1985

Source : MNHN, Paris

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Source : MNHN, Paris

Date de distribution : 18 novembre 1988.
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Alain Dubois, Maître de Conférences at the Muséum national d'histoire naturelle, Paris, is specialized in the study of Amphibia. He has devoted many works to the study of their systematics, evolution and biogeography, particularly in Europe and in Asia, where he has conducted field work over a number of years. He is also the author of several theoretical works dealing with various general problems of zoology and of evolutionary biology. He presents here a reflection on the notion of genus in zoology, and advocates an evolutionary concept of the latter : conceived as genetic, phylogenetic and ecological units, genera are real evolutionary units in nature. A new criterion is proposed to recognize genera : that of hybridizability.

ÉDITIONS
DU MUSÉUM
38,
RUE GEOFFROY
SAINT-HILAIRE
75005 - PARIS
1988
ISBN . 2-85653-151-2
ISSN . 0078-9747

PRIX : 156 FF TTC (France)
150 FF (Étranger)

Source : MNHN, Paris